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ON THE

STRUCTURE OF EUSTHENOPTERON

BY

W. L. BRYANT

BUFFALO, NEW YORK
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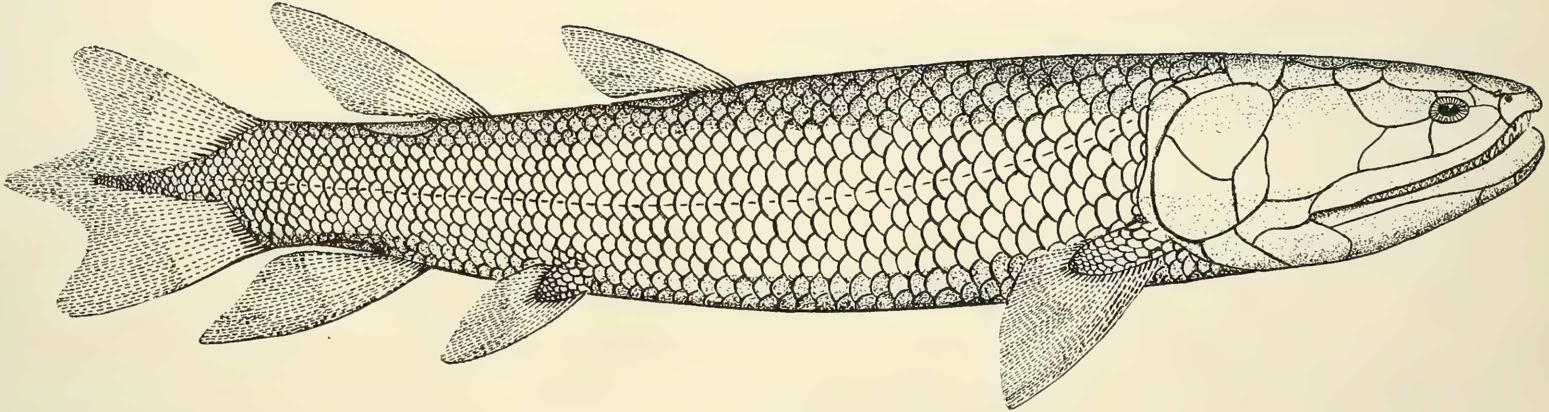

Text fig. 1. Eusthenopteron foordi, Whiteaves. Restoration of whole fish.

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ON THE STRUCTURE OF EUSTHENOPTERON

BY

WILLIAM L. BRYANT.

The origin and development of the various organs which together compose the marvelous human machine is the most interesting problem of Palaeontology. The geologist reconstructs, as on a stage, the historical settings which the palaeontologist peoples with strange and bizarre creatures acting the great drama of the ages. These ancient creatures, sluggish or rapacious, possessed in common that mysterious and unconscious force which insured to certain of their descendant races unlimited physical and mental progress.

The skeletal remains of these extinct animals reveal to the inquirer the development of the brain, of the sense organs; the slow modification of the limbs as they crept from the water to the land, and the persistent progressional change and adaptation of one organ after another to new functions caused by the exigencies of environment. Every skeleton from the far distant past has its own silent story for those who care to learn.

The studies embodied in this paper had their inception in my desire to illustrate the large collection of Devonian fishes in the Museum of the Buffalo Society of Natural Sciences with a series of restorations illustrating the fish life of the Devonian in America. The upper Devonian rocks in the vicinity of Scaumenac Bay, Quebec, contain a typical assemblage of fishes of the period for the most part in a good state of preservation; and in 1914 I visited that locality and made large collections. Subsequently two other collections were acquired by purchase, and Dr. John M. Clarke, Director of the State Museum, kindly placed at my disposal the State's very extensive series of fishes from the same locality, numbering many hundred individuals. I also visited the museums of London, Edinburgh, Montreal and Quebec for the purpose of studying their collections.

While the fossil fishes of Scaumenac Bay are usually much crushed, they are often found entire and the larger ones can sometimes be sectioned and worked out in such a way as to display their skeletal anatomy to better advantage than can the fossil fishes of the same age from any other locality of which I am aware. For instance, it is only recently through the researches of Watson and Day that anything has been learned of the internal skeleton of the head of the so-called Crossopterygian fishes of England. That little hardly prepared me for the remarkable conditions found in Eusthenopteron.

Modern research points to the Crossopterygii as being more nearly related to the projenitors of the air-breathing vertebrates than were the lung fishes; and on account of the morphological interest of this family I have made my studies of Eusthenopteron as elaborate as possible.

More than one author, including the late Dr. Whiteaves, the discoverer of Eusthenopteron foordi, has published restorations of this fish. The best of these appeared in Ray Lankester's "Guide to the Gallery of Fishes of the British Museum" in 1908. All of them, however, give inaccurate representations of its proportions, as they show the fish as though it was crushed flat, making it appear altogether too deep in proportion to its length.

Eusthenopteron (Text fig. 1 and Plate 1, fig. 1) was a rather slender, round-bodied fish resembling in its proportions Osteolepis rather than Holoptychius. That it was an active, voracious animal of predatory habits may be inferred from its elongated gape and the massing of the large fins at the posterior portion of the trunk.

Its head occupied about one quarter of its length and its greatest depth was contained a little more than five times in its total length. Its dorsal, ventral and anal fins were placed rather far back, the ventrals being located about midway between the first and second dorsals, and the anal fin somewhat behind the second dorsal.

A single, enlarged ridge scale occurs immediately behind each of the dorsal and the anal fins. Watson and Day (1916, p. 25) believe that these scales, present in nearly all members of the family, have arisen through the disarrangement of the squamation due to the reduction in the width of the insertion of the fins, following the concentration of their endo-skeletal supports.

The body was covered with rather small cycloidal scales. On Plate 16, I have figured a portion of the squamation of Eusthenopteron foordi and below it for comparison, that of Holoptychius quebecensis from the same locality.

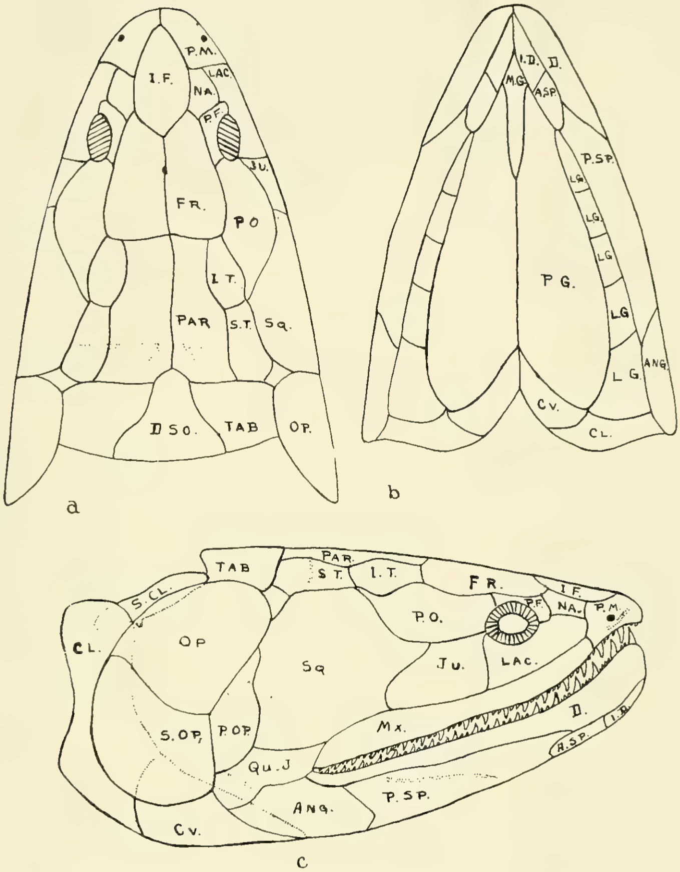
The minute structure of the scales of Eusthenopteron does not agree with that of the cosmoid scale as defined by Williamson (1849 and 1850) and Goodrich (1909, p 214) and said to occur only in the Dipnoii and Crossopterygii; neither can it be said to be a true ganoid scale. On Plate 18, figs. 1 and 2, I have figured magnified sections; on Plate 17, fig. 1, one of the ornamental tubercules more highly magnified; and for comparison with these, on Plate 18, figs. 3 and 4, I give sections of scales of Holoptychius quebecensis. None of these sections show the conditions said to obtain in either the Crossopterygii or the Dipnoii nor, on the other hand, do they seem to resemble typical ganoin scales.

The scale is formed of three layers of true bone with bone cells everywhere present. There is neither any trace of dentine or of the modified dentine known as cosmine, nor so far as I can find is there any such structure as vitrodentine, enamel or ganoin. There is a lower layer of bony lamellae of the type known as isopedin, penetrated by horizontal canals; a middle layer of vascular bone, and an upper layer of very dense isopedin, in which the matrix is deposited in successive layers with bone cells in parallel planes. At the extreme end of the scales the vascular layer disappears and the upper layer slopes downward to fuse with the lower. This condition is almost exactly paralleled in the dermal scutes of the Antiarchi; for instance in Bothriolepis canadensis from the same formation, the magnified section of whose shield figured by Goodrich (1909, p. 206) might well serve to illustrate that of Eusthenopteron. It seems to me remarkable that fishes so closely related as Eusthenopteron and Megalicthys should differ so remarkably in the structure of their dermal plates; the former resembling that of the Antiarchi, while the latter has the complex structure of the Pteraspidae.

In this simple lammelar, bony structure of the outer layer of the dermal defenses of Eusthenopteron is probably to be found the reason for the fusion of the outer surface of certain head plates, for instance, those covering the snout and cheeks, where such fusion is complete externally but internally the sutures may still be detected. Owing to this fusion of the external surfaces of many of the dermal bones of the skull their true outlines are more readily made out in their inner aspect.

This fact has a somewhat important bearing upon the question of the origin of the dermo-cranium in fishes. Dr. Gregory (1915, p. 327) in support of his "fragmentation" theory, instances the continuous rostro-frontal shield of Osteolepis as more primitive than that of types in which paired nasals and other plates appear in that region. Now as Dr. Broom has remarked, the test that must be applied to all theories of this sort, is how did the intermediate stages work? The conditions in Eusthenopteron, however, indicate that whatever may have been their origin there was in this family a progressive or secondary fusion of elements; that this fusion took place at first in the outer layer; and that the more primitive members of the family were those in which the dermal elements were the most numerous. The development of the exoskeleton thus parallels that of the endoskeleton as shown for instance in the progressive fusion of fin elements.

Text fig. 2 shows the skull of Eusthenopteron in dorsal, ventral and lateral views. At the posterior end of the skull in its dorsal



Text fig. 2. Skull Pattern of Eusthenopteron foordi Whiteaves. a dorsal, b ventral and c lateral view. Ang., Angular; A. Sp., Anterior splenial; Cl., Cleithrum; Cv., Clavicle; D., Dentary; D. So., Dermosupraoccipital; Fr., Frontal; I. D., Infradentary; I. F., Interfrontal; I. T., Intertemporal; Ju., Jugal; Lac., Lacrymal; L. G., Lateral Gular; M. G., Median Gular; Mx., Maxilla; Na., Nasal; Op., Operculum; Par., Parietal; P. F., Prefrontal; P. G., Principal Gular; P. M., Premaxilla; P. O., Postorbital; P. Op., Preoperculum; P. Sp., Posterior Splenial; Qu. J., Quadratojugal; S. Cl., Supracleithrum;; S. Op., Suboperculum; Sq., Squamosal; S. T., Supratemporal; Tab., Tabulare

(Sensory canals indicated by double dotted lines.)

aspect there is a large subtriangular median bone, the dermosupraoccipital, on each side of which are the quadrangular tabulars. In advance of these are the long and rather narrow parietals, bounded on either side by two smaller bones, the intertemporal and the supratemporal. These six latter bones were firmly united by sutures into a continuous shield nearly flat on top and curved on the sides. In adult individuals the sutures are obliterated externally and the individual bones are only obscurely indicated by the arrangement of the ornament.

In advance of the parietals and loosely articulated to them and to the intertemporals are the frontals. These are closely united by a suture in the median line except at one point about opposite the posterior margins of the orbits where there is a pineal opening. As it is not elevated above the surrounding surface externally and there is no modification in the arrangement of the ornamental tubercules the opening is more readily observed from below, where it is wider. It is well shown in the specimen photographed on Plate 3, fig. 2. The frontals are notched anteriorly to receive the large median bone which I call the interfrontal, and which may be the homolog of a median ossification occuring in the Palaeoniscidae, sturgeons and many teleosts i. e., the tarpon, and called by Traquair the super-ethmoid.

This membrane bone is sometimes named mesethmoid by authors in teleosts, but the true mesethmoid is a cartilaginous element lying beneath it. "It has very much the position of the dermal bone named by Broom interfrontal in Eryops, except that in Stegocephalians, in correlation with the great extension of the olfactory region, the nasals have gained contact in front of the interfrontal, which is now a small element and subsequently disappears." (Gregory, 1918.)

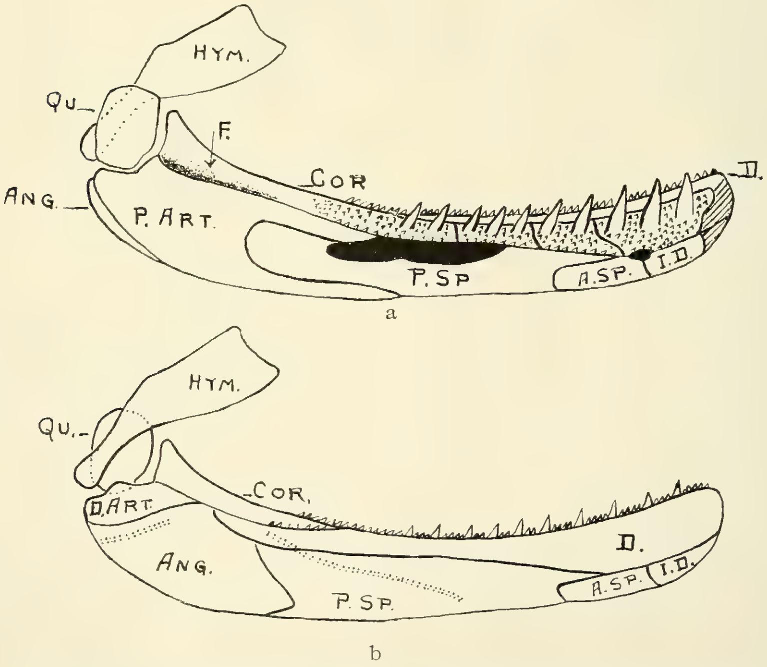
There is a singular lack of rigidity in the connection between the parietals and frontals which is remarkable in view of their relation to the brain case. In Osteolepis also, what seems to be a pineal foramen occurs at a point between the frontals far in advance of their junction with the parietals. This apparently flexible union between the frontal and parietal regions occurs in other members of the family i. e., Holoptychius and Glyptopomus. In the fossils there is nearly always a dislocation at this point which causes the front of the skull to appear more depressed than was actually the case in life. I shall have occasion to refer again to this peculiar structure in my description of the brain case and palate. This portion of the head-shield is illustrated in Plate 5, fig. 2; and fig. 3 on the same plate shows to good advantage the shape of the interfrontal. Two large premaxillæ in advance of the interfrontal fuse with it and with the two small nasals to form a continuous shield over the snout, in which the sutures are externally almost entirely obliterated. The external nostrils are located in the premaxillæ, slightly in advance of the nasals. In one specimen I have seen indications of another small polygonal bone wedged in between the interfrontal, the nasal and the premaxilla, but as I am not certain about it I have not indicated it in my restoration. The rather small orbits are bounded above by the narrow prefrontals which are curved to conform to their shape. On Plate 2, fig. 1, I show a rather well preserved skull which exhibits very clearly the position of the eye and of the external nostril. Figs. 2 and 3 on the same plate show that the eye was defended by an inner ring of true sclerotic plates which are closely articulated, and conform to the shape of the eye-ball. The nostril is seen to be located some distance in front of the eye and is laterally, not ventrally, directed.

Behind the orbit is a large bone, the postorbital, which is in contact dorsally with the frontal and is continued as a narrow wedge between the intertemporal and a large cheek plate, usually named the squamosal. It also articulates with the prefrontal and below with the jugal. The squamosal is the largest of the cheek plates. It is so firmly united to the preoperculum and to the quadratojugal that the sutures can only be detected by an examination of their inner surfaces. This aspect is shown on Plate 5, fig. 1, and the preoperculum and quadratojugal in this species have never before been positively recognized. It is probable that better material would show their presence in all of the members of this family although they are said to be absent in Gyroptychius and Osteolepis.

The preoperculum is an elongated bone, narrow above, articulating behind with the large operculum and suboperculum and below with the quadratojugal, in advance of which is a long and slender maxilla. The remainder of the cheek above the maxilla is occupied by two large bones, the jugal and the lacrymal, the latter of which forms the lower border of the orbit and is in contact besides with the prefrontal, nasal and premaxilla.

Wedged in between the squamosal, the operculum, the tabular and the supratemporal, is a small bone which has also been observed in Holoptychius and Glyptopomus. This evidently represents an imperfect development of the transverse series of small quadrangular bones which in Osteolepis macrolepidotus, as shown on Plate 6, fig. 1, cross the skull immediately behind the parietals and supratemporals. Dr. Gregory (1915, p. 329) in his discussion of these elements has given excellent reasons for declining to consider them as homologs of the transverse post-parietal series in the Stegocephali and with this opinion I am inclined to concur.

It is very difficult to make out the individual bones on the external surface of the mandible as the sutures are mostly closed. However, after examining a very large number of specimens, I believe that I am safe in representing them as in Text fig. 3. The derm-articular appears on the outer surface as a narrow strip of



Text fig. 3. Eusthenopteron foordi, Whiteaves. Ramus of lower jaw in a, inner aspect; b. outer aspect. Ang., Angular; A. Sp., Anterior Splenial; Cor., Coronoid; D. Art., Derm-articular; D. Dentary; F., Fossa for adductor mandibulae; Hym., Hyomandibular; P. Sp., Posterior Splenial (above which is a large mandibular vacuity); Qu., Quadrate.

bone wholly covered by the quadratojugal. Below this is the angular which is followed in front by a large posterior splenial; and in advance of this the lower border of the jaw is completed by two narrow bones, the anterior splenial and the infradentary. These two bones can easily be made out on a pair of large mandibles belonging to the New York State Museum figured on Plate 3, although they are not conspicuous in the photographs. They are also to be observed in inner and outer view on the mandible figured on Plate 7. The dentary is a long bone expanded in front, narrow behind, its upper border studded with minute teeth.

On Plate 11 I have figured an interesting specimen of Holoptychius quebecensis, Whiteaves, which displays in inner view the principal and lateral gulars together with a pair of imperfect mandibles. Only the outer bones of the mandible are preserved, but these confirm, to a great extent, the structure of the mandible of Eusthenopteron; and Dr. Hussakof and I (1918) have recently figured a mandible of the remarkable Crossopterygian, Onychodus which indicates a somewhat similar arrangement.

The inner surface of the mandible being destitute of ornament is much more easily made out. Lying within and below the margin of the dentary there is a series of coronoid bones studded with minute teeth and supporting a row of large tusks. The posterior of these bones is the longest and terminates behind in a process which articulates with the quadrate and is separated from the prearticular by a large fossa for the aductor mandibulae. The prearticular is also in contact with the quadrate and is notched anteriorly to receive the elongated posterior splenial. The angular appears as a narrow strip of bone at the posterior lower margin of the jaw. Above the posterior splenial is a large mandibular vacuity. The anterior splenial and infradentary complete the lower margin of the jaw in front. There is a small foramen just above them.

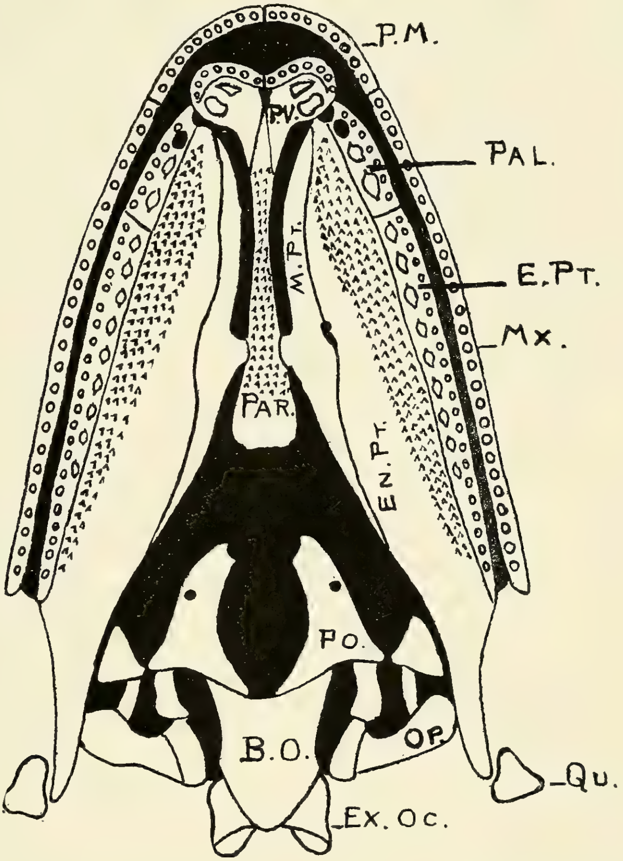
The mandible of Eusthenopteron thus shows a most striking and remarkable resemblance to that of a primitive amphibian, for instance that of the Stegocephalian Trimerorhachis, even to the position of the various foramina; a resemblance which is further heightened as I shall later show by the minute structure of the teeth.

The quadrate is a small bone lying in the angle of the jaw, rather thick behind, over-lapped externally by the hyomandibular, which is an elongated bone somewhat expanded above, cylindrical below, descending obliquely downwards and backwards, slightly bent a little below the middle, at which point there is a process for articulation with the operculum. The hyomandibular resembles very much its homolog in the Palaeoniscidae. I have not noticed a foramen in this element. This and the quadrate are well shown on Plate 4. I have seen no specimen in which I could positively identify a sympletic, although it may have been present.

On the ventral surface of the head there is a pair of large conspicuous principal gulars in contact with each other for a portion of their length, but divided anteriorly by a narrow median gular. The principal gulars are figured on Plate 6, fig. 2, where the median gular has disappeared but the flanges for its reception are clearly shown. The principal gulars which are much narrower than their homologs in Holoptychius (cf. Plate 11, fig. 1), are bordered externally by a row of lateral gulars. These are rarely to be seen in the fossils. In the specimen figured on Plate 3 they have been mostly destroyed, but their position is indicated by the gap and flanges between the mandibles and the principal gulars. They are six in number, expanding gradually toward the rear. The clavicles are inserted between the posterior expanded portions of the principal gulars.

The sensory canals on the head of Eusthenopteron are not nearly so conspicuous as in other members of the family, nor do they correspond in position entirely with those of Osteolepis, Diplopterus and Holoptychius. A transverse canal arising at a point near the suture between the parietals extends across the skull on each side, traversing the parietal and supratemporal and disappearing near the upper margin of the squamosal. From this canal a short branch arising near the inner margin of the parietal leads diagonally backward in the direction of the operculum. There is a short horizontal canal just below the nostril on the premaxilla and another extending across the upper limb of the preoperculum. A short canal crosses the quadratojugal and another extends diagonally downward and forward traversing the posterior splenial of the mandible. The lateral line is conspicuous in many of the better preserved specimens. It arises near the upper border of the operculum and curving gently downward soon takes a horizontal direction along the middle of the trunk.

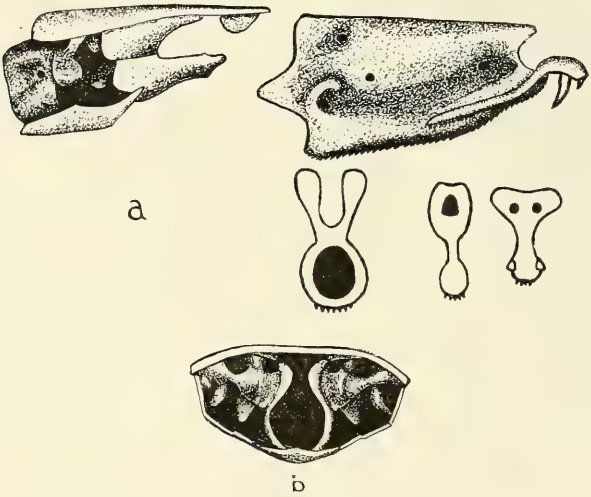
There are a number of specimens in the Buffalo Museum which afford considerable information concerning the skeleton of the brain case and of the palate. Just behind the premaxillæ (Text fig. 4) Plate 10, fig. 2 there is a large palatal vacuity. The prevomers are paired, triangular, rounded in front; and each bears a large tusk along side of which is a pit for its successor, although two of these tusks may be functional at the same time. Besides the tusks the prevomers are each armed with a single outer row of smaller teeth. Wedged between the two prevomers is a very deep



Text fig. 4. Skull of Eusthenopteron foordi, Whiteaves. Palatal aspect. B. O., Basioccipital; En. Pt., Entopterygoid; E. Pt., Ectopterygoid; Ex. Oc., Exoccipital; M. Pt., Metapterygoid; Mx., Maxilla; Op., Opisthotic; Pal., Palatine; Par., Parasphenoid; P. M., Premaxilla; Po., Prootic; P. V. Prevomer; Qu., Quadrate.

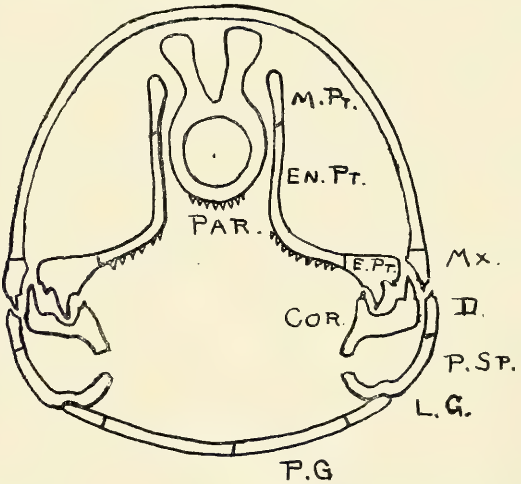
and narrow median bone expanded at its hinder end and above in front, which I assume to represent, at least in part, the parasphenoid; although it differs greatly from that in any other known fish. This element arises below the junction of the parietals and frontals and extends forward as a vertical double sheet of very thin bone which in life enclosed either a cartilaginous or a cancellous bony interior. This forms a complete interorbital septum and extends from the roof of the cranium to the mouth. Its lower margin is studded with a shagreen of fine denticles.

This element is much expanded posteriorly and is excavated into two chambers (Text fig. 5) opening backward, the lower one conical and pierced on each side by a foramen which opens externally into a recess just in advance of a lateral process; the upper chamber is trough-shaped, open above as well as at the rear and like the lower a foramen leads out of each side. There is another foramen a short distance behind the nasal chamber. Above the prevomers this bone suddenly expands and is excavated for the olfactory chambers which communicate with the surface through openings in the premaxillæ. One specimen which exhibits a



Text fig. 5. Eusthenopteron foordi, Whiteaves. a, Side view of brain case and interorbital septum, including vomerine and parasphenoidal regions; with vertical cross-sections at various points. The paired olfactory canals shown in the anterior section have united in that following. b, Brain case viewed from behind.

cast of the interior of this chamber shows that the mucous membrane was arranged in parallel folds like a rosette. From each of these nasal capsules a tube leads backward and, shortly uniting with its fellow, passes through the upper portion of the septum and opens as a single tube into the uppermost of the posterior vacuities before described. I have illustrated on Plate 9, figs. 2, 3 and 4, this bone in side and top views. Fig. 1 on the same plate shows its relation to the frontals and interfrontal. On Plate 10 it is seen, together with the prevomers, in ventral or oral view. I assume from comparison with the skull of Polypterus and of the sturgeon that the uppermost of the two vacuities in this element must represent the front part of the brain case. Then, too, the pineal opening is directly above its forward termination. As to the lower conical pocket I can only doubtfully surmise that it may have formed the front end of an eye muscle canal.



Text fig. 6. Skull of Eusthenopteron foordi, Whiteaves. Transverse section of a point near the posterior termination of the frontals. Roofing bones of skull are not indicated. Cor., Coronoid; D., Dentary; En. Pi., Entoptergoid; E. Pt., Ectopterygoid; L. G., Lateral Gular; M. Pi., Metapterygoid; Mx., Maxilla; Par., Parasphenoid; P. G., Principal Gular; P. Sp., Posterior Splenial.

Text fig. 6 is a transverse section of the skull in the region of the frontals, largely founded upon a single specimen in which the bones were fairly well preserved in their mutual relations.

I have said that the element, median in the trabecular region, represents in part the parasphenoid of other ganoids and of teleosts. That this is true is proved by the fact that its ventral margin is studded with minute denticles. That it terminated just below the junction of the frontals and parietals is positively demonstrated by many specimens in the Buffalo Museum in which all the parts are preserved in their natural relation to each other and in which the delicate bones comprising the brain case are hardly crushed or distorted. It includes, however, the whole sphenethmoid (ethmoid and orbitosphenoid) region, although I have been unable positively to make out any sutures; and the upper walls form the front part of the brain case.

In this connection I shall quote from a letter from Dr. William H. Gregory to whom I am greatly indebted for advice: "The profound differences from Polypterus are very surprising. Possibly they may indicate merely that Polypterus has become ichthyized or converged toward normal fish-like conditions in the millions of years since the upper Devonian. It may well be that the backward extension of the parasphenoid so as to cover the back part of the skull base is in some way correlated with the peculiar specialization of the eye muscles which builds up the myodome or muscle canal in modern fishes. Assuredly this condition must be a secondary one because it traverses the region formerly occupied by the connection between the hypophysis and the base of the brain, and secondly because the parasphenoid is a dermal element representing a part of the stomadaeum or in-pushing of surface tissue. Your fish would then represent a stage in which this in-pushing in the mid-line had not yet extended behind the infundibulum-hypophysis, while the denticulate tract of the pterygoid and ectopterygoid shows that at the sides this in-pushing had extended back nearly to the quadrate.............This stage must have been passed through by the earlier fishes, but whoever dreamed of finding it in a real specimen?"

Dr. Sagemehl (1883) in his discussion of the cranium of Amia remarks that in ganoids and dipoans the parasphenoid does not terminate at the base of the true skull but extends backward beneath several vertebrae—as many as seven or eight in Polypterus—and thinks that this must have been also the case in the direct ancestors of the existing bony ganoids and teleosts; and that in later times a curtailment from behind took place causing a reduction in number and consolidation of the vertebra resting upon this bone, which was already firmly connected with the cranium; a trasformation the last stages of which can still be seen in recent fishes.

The skull of Eusthenopteron seems to me to show conclusively that Dr. Sagemehl was wrong in this assumption, at least in so far as the Crossopterygii are concerned, and that rather the opposite was the case is the more easily imagined when we recall that the para-basisphenoid in Permian ganoids and in modern snakes is a compound bone resulting from the fusion of at least three elements. (Henry Day, 1915).

The metapterygoid (Plate 8, fig. 2; Plate 9, fig. 4) is a long subtriangular bone bearing on its thickened upper margin two processes, one of which may have articulated with the median bone just described, while the other suggests that it articulated with the side of the skull more or less after the fashion of an amphistylic shark. (Goodrich, 1909, p. 190, fig. 159). It is never in contact with its fellow of the opposite side. It occupies a nearly vertical position and is welded by a very long suture to the entopterygoid. This is a thin sheet of bone, concave outwardly and terminating in front in a spatulate process which rests upon the expanded prevomers, while behind, it lies against the inner side of the quadrate. It agrees in a general way with Watson's description of the pterygoidal element in Glyptopomus and Rhizodopsis. The bone is nearly vertical in its upper and posterior portions, but suddenly curves outward in a nearly horizontal flange to meet the ectopterygoid and palatine to which it is firmly united by suture. On its lower surface it is covered with minute denticles. On Plate 8 it may be seen in dorsal and lateral views together with the metapterygoid, ectopterygoid and palatine. It is also shown on Plate 9, fig. 4.

The ectopterygoid is a long quadrangular and robust bone, bearing on its oral margin an inner row of laniary teeth with a row of smaller teeth outside of them. Fig. 3 on Plate 7 shows a cross-section through this bone and its teeth and on Plate 17, figs. 2, 3 and 4, I have figured cross-sections of various teeth to show the labyrinthine infolding of the walls. It becomes more and more complicated toward the base.

In front of the ectopterygoid is the palatine, a similar bone but shorter. It also bears two or three tusks and is connected by a finger-like process to the prevomer. There is a foramen (shown in the specimen figured on Plate 9, fig. 4), near the anterior margin of the palatine, which communicates with the mouth and seems to be a passage for the internal nares.

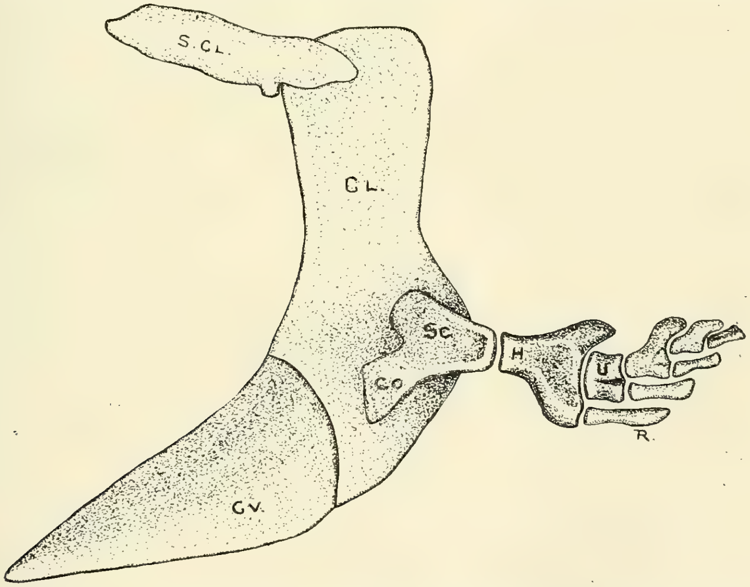
Behind the parasphenoid there is a large vacuity bounded on either side by two, more or less triangular bones, each of which is perforated by a foramen. Their position and the presence of this foramen suggest their homology with the prootics of modern fishes, and I have so named them. The outer and hinder margins of the prootics articulate with a small quadrangular bone (shown in side view on Plate 9, fig. 3), which extends nearly vertically downward from the roof of the skull in the region of the supratemporal. They are also connected behind with a median shield-shaped bone which, it seems to me, represents the basi-occipital. I have figured this portion of the skull in ventral aspect on Plate 14, figs. 4 and 5. Fig. 2 is an upper view of the same specimen showing the relation of these bones to the parietal region, while fig. 3 on the same plate shows it from the rear.

Above the basi-occipital and extending to the roof of the skull is a pair of curved bones similar in every respect to the lateral elements of the vertebral centra, except that they are wider; and which I have called the exoccipitals. Like the centra they each bear on their outer surfaces a wide vertical sulcus. Each of them is perforated by a small foramen and each is in contact at its forward margin with a dumb-bell shaped bone which extends upward and outward to the roof of the skull. I am unable to offer any opinion as to the homology of this latter pair of bones except that they resemble in shape and position the paroccipitals in Trimerorhachis as figured by Broom (1913, p. 572, fig. 6) and might therefore represent the opisthotics of fishes; but indeed, all of the bones of the posterior half of the brain case are so vastly different from those of any known fish or amphibian as to defy positive identification.

Besides the bones I have described there are two other paired elements to be seen in the specimen shown on Plate 14, figs. 4 and 5. One of them connects the prootic with the inner margin of the dumb-bell shaped bone, the other connects the outer margin of the last mentioned bone to the quadrangular element below the supratemporal just in front of which seems to have been the attachment for the hyomandibular.

I shall not at this time discuss the significance of the fact that we have in the base of the skull of this remarkable fish a median ventral opening in the region of the hypophysis and whether we have here vestiges of a former connection between the pharynx and the base of the brain, and all that this might imply in relation to the derivation of the vertebrates.

On account of the extremely interesting structure of the pectoral fin of Eusthenopteron it has often been figured by authors who have found in it more than a suggestion that the amphibian limb originated from a somewhat less specialized ancestor of the Crossopterygians. The best of these illustrations are those published by Broom (1913) and Petronievics (1918). I can add something to our knowledge of this fin for there is in the Museum of the Buffalo Society a specimen which I illustrate on Plate 14, fig. 1, and which exhibits a nearly complete shoulder girdle with the scapulo-coracoid very much in its natural position; and as the scapular element has never before been found in Crossopterygian fishes I give in Text fig. 7 a drawing of the pectoral girdle with the fin elements attached. The supra-clavicle is a



Text fig. 7. Eusthenopteron foordi, Whiteaves. Right pectoral limb, medial aspect. Co. Sc., Coracoscapula; Cl., Cleithrum; Cv., Clavicle; H., Humerus (basal piece of mixopterygium); R., Radius; Sc., Scapula; S. Cl., Supracleithrum; U., Ulna.

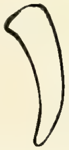
narrow elongated bone, and from its lower margin arises a process which articulates with the cleithrum. The cleithrum is the largest element of the girdle and externally overlaps the clavicle, a triangular element with no upwardly ascending process such as has been found in Rhizodus. The scapulo-coracoid is a rather small element tapering behind where it is abruptly thickened. Its posterior face is excavated to articulate with the single proximal piece of the limb which Broom, Gregory and others consider to be homologous with the humerus of the tetrapoda. This scapular element is, indeed, somewhat like that in Polypterus, except, that the coracoid is apparently not a distinct bone. On Plates 11 and 12 I have illustrated the left pectoral fin, with its skeletal supports. Fig. 1 on Plate 12 shows the best specimen of this fin I have ever seen and, fortunately, most of the elements of the right pectoral are preserved in the same specimen.

It is seen by an examination of this fin that there are five axial pieces instead of the four shown in the British Museum example figured by Pietronievics; and three postaxial processes instead of two. These postaxial processes are certainly not distinct elements, the haversian canals leading up to the center of ossification in the main body of the axinost. Neither do I find that the fourth axinost is bifucrated as supped by Pietronievics. It has a postaxial process as indicated in Broom's figure and articulated to its main body distally is a fifth axinost. This, as well shown in its mate of the right side is small, robust, constricted in the middle; and a longitudinal groove like that in the second axinost shows interesting traces of the concentration of elements which has taken place in this fin; thus the mesomere thought by authors to represent the ulna is very evidently made up by the fusion of two or more elements. Fig. 2 on Plate 11 shows the squamation of the fleshy lobe of the fin as well as the tubercular ornament of the scale-like rays.

The endo-skeletal supports of the pelvic fin are not very well preserved in any of the specimens which have come under my notice. They have, however, been heretofore illustrated by Goodrich. Plate 13 shows the pelvic bones in their natural association behind which is a peculiar arrangement of a portion of the squamation which I assume marks the position of the vent. On Plate 1, fig. 2, may be seen a specimen which shows the supports of the dorsal and anal fins; and on Plate 12, fig. 2, is illustrated another specimen showing the supports of the anal, second dorsal and caudal fins.

As is well known, the dermal rays of the upper or epichordal lobe of the caudal fin are supported directly upon the elongated neural spines while those of the hypochordal fin are supported by interspinous bones. There is, however, some question as to whether the large bones bearing the three ossicles which support the first and second dorsal fins are interspinous in character. Whiteaves thought they were, and in this view he was upheld by Traquair (1890, p. 15); and Hussakof (1912, p. 128) in a recent figure of a large fish in the New York State Museum indicates that the second dorsal fin was supported by three ossicles articulated to a larger interspinous bone. However, in all of the specimens which are at present before me, this does not appear to be the case and so far as can be made out from the specimens, the first and second dorsal fins are each supported by a large club-shaped bone which appears to be attached directly to the vertebral centra, as a modified neural spine. Plate 1, fig. 2, shows these bones in what is apparently their natural position and my assumption that they are, indeed, neural spines is supported by the fact that this element of the first dorsal fin bears on its upper surface a process (zigapophysis) which is also to be seen in the smaller neural spines. The corresponding bone in the anal fin is, however, like those supporting the lower lobe of the caudal, an interspinous bone.

I find that the vertebral centra of Eusthenopteron are not, as has been supposed, ossified into complete rings. They are rarely perfectly preserved. Each centra is made up of two lateral pieces which are not in contact with each other either above or below. There is a conspicuous vertical sulcus on each outer surface as is also the case in the exoccipitals. Text fig. 8 is a vertical cross-section of one element. It is thickest above and tapers ventrally.



Text fig. 8. Section of one-half of vertebra.

On Plate 15 I have figured various centra from portions of the trunk associated with their neural arches. I have never seen indications of any interdorsal elements. Fig. 1 shows that these arches were produced above into broad, flattened and robust spines closely opposed. I am unable to say anything about the haemal spines of the trunk further than that they were smaller and more slender and pointed than those of the dorsal side.

This ends my account of the skeletal structure of Eusthenopteron and I conclude with the hope that students of morphology will be interested by the profound and suggestive differences separating the Devonic Crossopterygii from even such generalized modern fishes as the Polypterini.

LIST OF WORKS CITED.

BROOM, R., 1913. "On the Origin of the Cheiropterygium." *Bull. Am. Mus. Nat. History,* Vol. 32, 1913.

Ibid. 1913. "Permian Temnospondylous Stegocephalians of North America." *Bull. Am. Mus. Nat. History,* Vol. 32, 1913.

DAY, HENRY, 1915. "A Note on the Parasphenoid of A Palaeoniscoid." *Ann.* & *Mag. of Nat. Hist.,* Ser. 8, Vol. xvi, 1915.

GOODRICH E. S., 1909. A Treatise on Zoology, Part IX, London, 1909.

GREGORY, W. K., 1915. "Present Status of the Problem of the Origin of the Tetrapoda. *Ann. N. Y. Acad. Science,* Vol. xxvi, 1915.

Ibid. 1918. Letter to Author.

HUSSAKOF, L., & BRYANT, W. L., 1918. "Catalog of the Fossil Fishes in the Museum of the Buffalo Society of Natural Sciences." *Bull. Buffalo Soc. of Nat. Sciences,* Vol. XII.

HUSSAKOF, L., 1912. "Notes on the Devonic Fishes from Scaumenac Bay." *Bull. N. Y. State Museum,* 158, 1912.

LANKESTER, RAY, 1908. "Guide to the Gallery of Fishes of the British Museum, 1908."

PETRONIEVICS, BRANISLAV, 1918. "Notes on the Pectoral Fin of Eusthenopteron." *Annals & Mag. of Nat. History,* Ser. 9, Vol. ii, Dec., 1918.

SAGEMEHL, DR., 1883. Translated in R. W. Shufeldt's paper "On the Osteology of Amia Calva." *Washington,* 1885.

TRAQUAIR, R. H., 1890. "Notes on the Devonic Fishes of Scaumenac Bay and Campbellton, Canada." *Geol. Magazine,* Dec. 3, Vol. 7, 1890.

WATSON & DAY, 1916. *Mem.* & *Proc. Manchester Lit.* & *Phil. Soc.,* Vol. LX, Pt. 1, 1916.

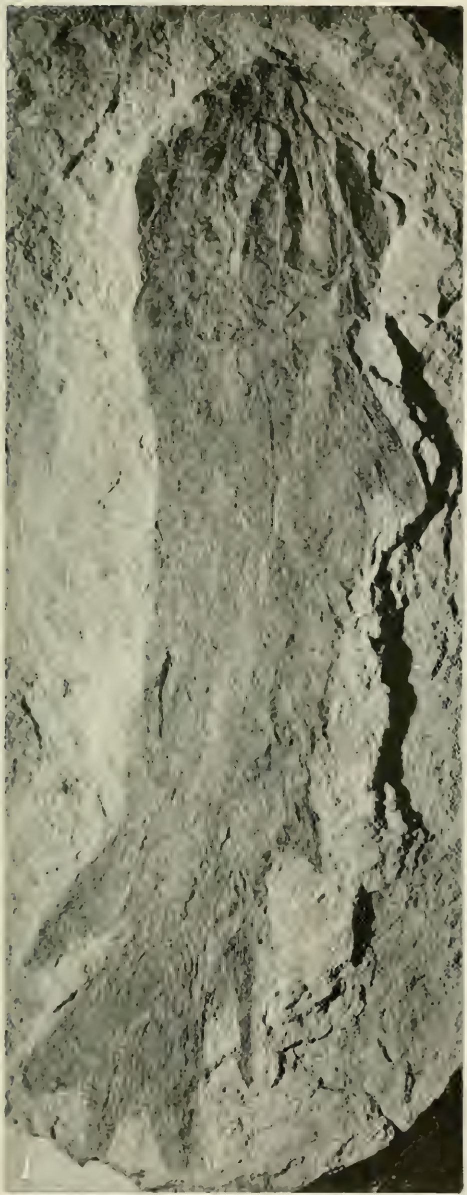
WILLIAMSON, W. C., 1849, 1850. "Structure of Scales of Fishes, etc." *Part I, Phil. Trans.,* Vol. cxl, 1849; Part II, ibid, vol. cxli, 1850.

PLATE 1.

Eusthenopteron Foordi. Whiteaves.

Fig. 1. Complete fish showing position of fins and of the lateral line.

Fig. 2. Skeleton of caudal portion of the trunk showing neural and haemal spines and the supports of the dorsal and anal fins.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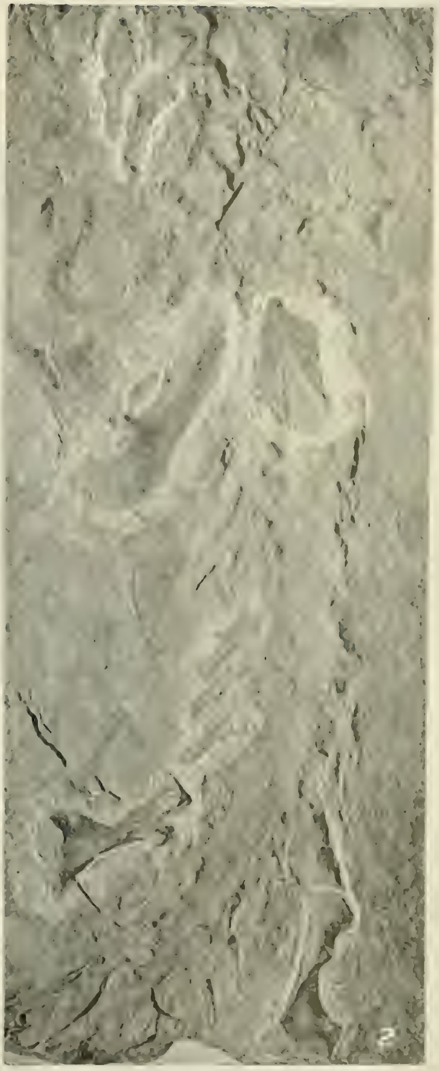
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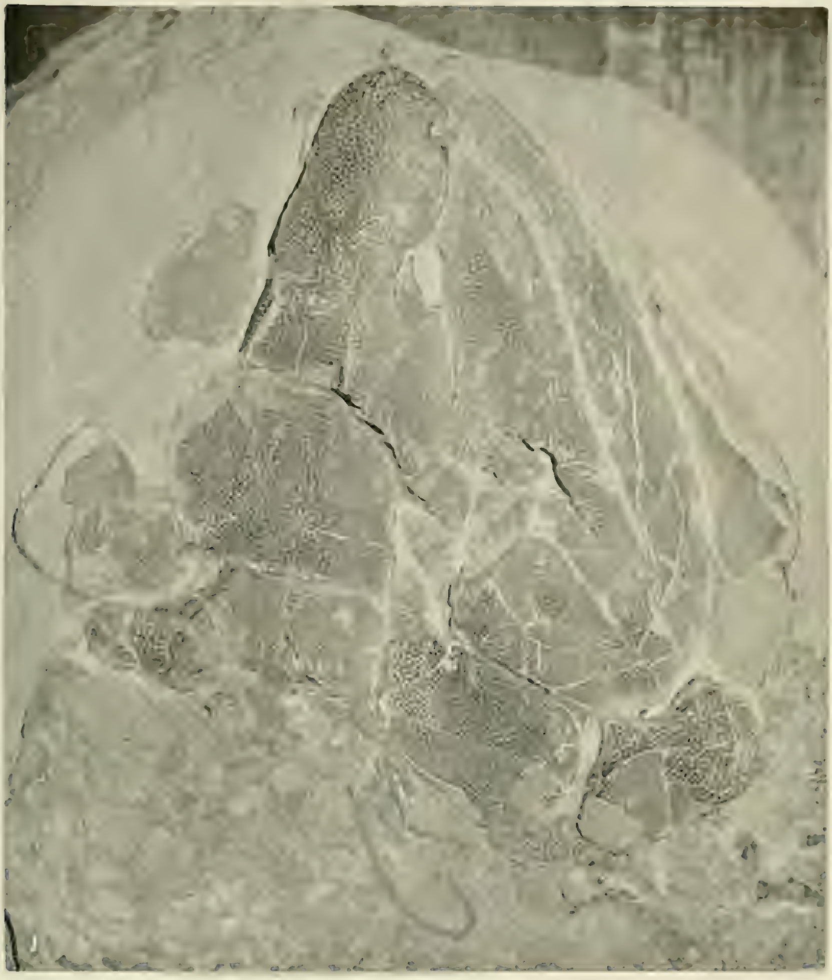
PLATE 2.

Eusthenopteron Foordi, Whiteaves.

Fig. 1. Crushed head of large individual, showing sensory canals, position of the orbit and nostril.

Fig. 2. Crushed head of small individual showing ring of sclerotic plates.

Fig. 3. Enlarged view of sclerotic ring shown in fig. 2.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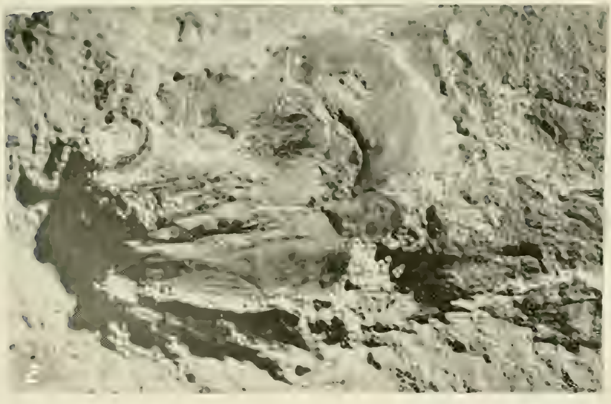
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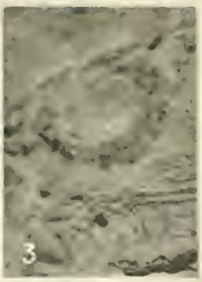
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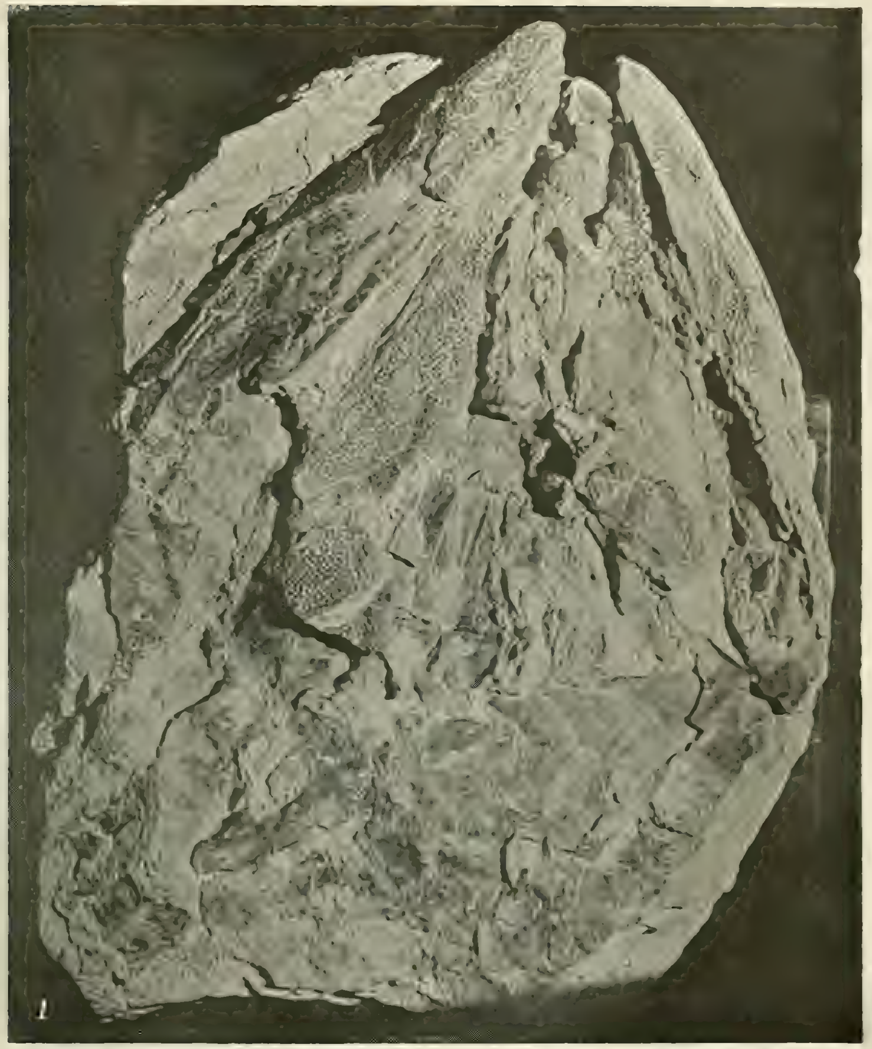
PLATE 3.

Eusthenopteron Foordi, Whiteaves.

Fig. 1. Head seen from below showing mandibles and the principal gulars.. The lateral gulars have mostly disappeared but their position is indicated by the gap between the mandibles and the principal gulars. Between the separated principal gulars may be seen the posterior termination of the parasphenoid.

Fig. 2. Inner view of cranial roofing bones showing well the pineal foramen between the frontals.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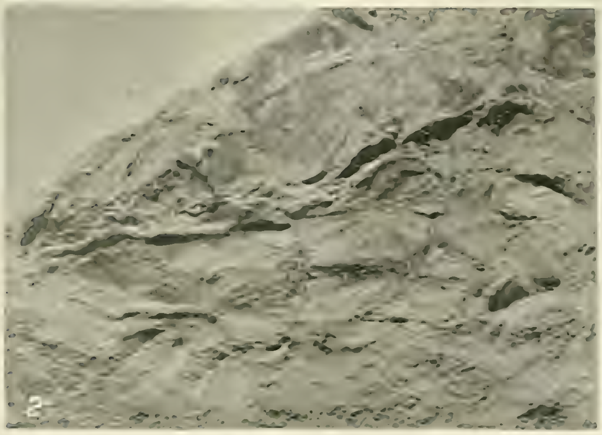
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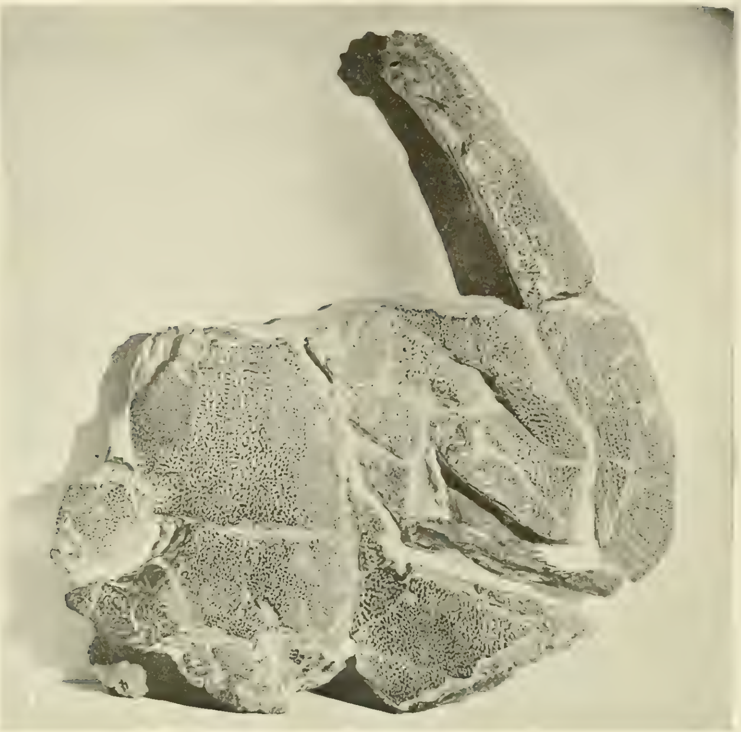
PLATE 4.

Eusthenopteron Foordi, Whiteaves.

Fig. 1. Right mandible and hyomandibular in outer view.

Fig. 2. Inner view of the same specimen showing as well the quadrate bone of the right side, the left hyomandibular and the left cleithrum, clavicle and supports of the left pectoral fin.



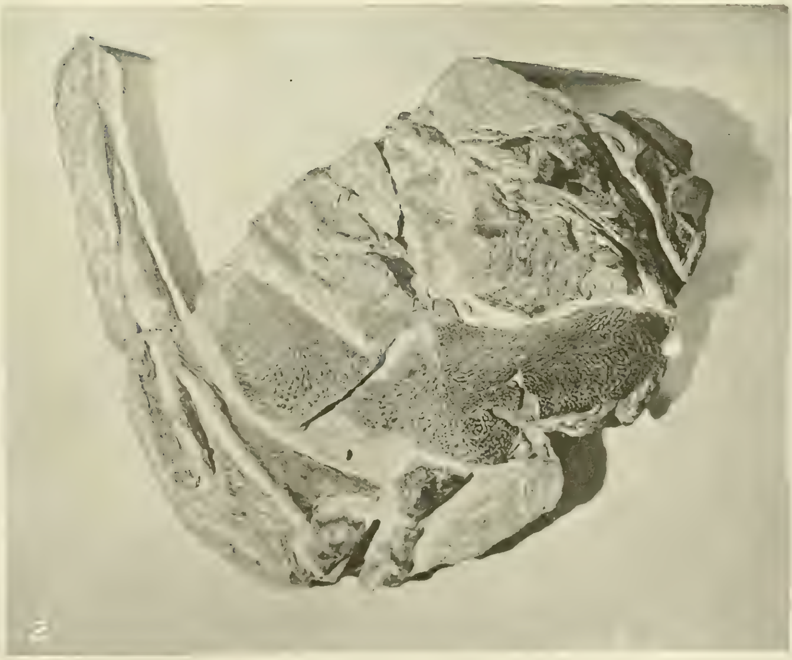


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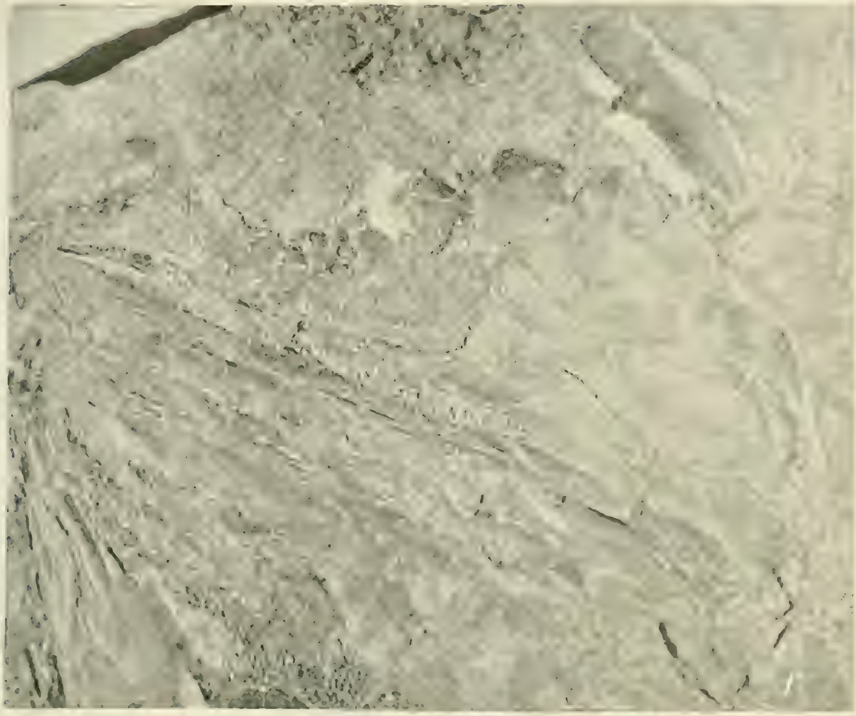
PLATE 5.

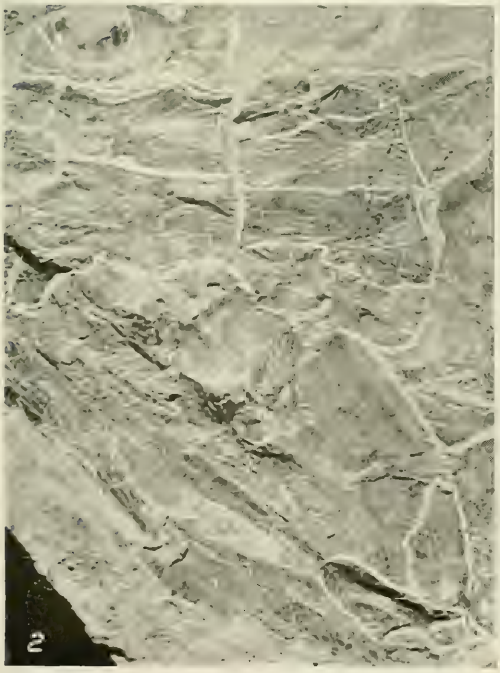
Eusthenopteron Foordi, Whiteaves.

Fig. 1. Inner view of the cheek plates showing the preoperculum, quadratojugal, squamosal, maxilla, mandible, etc.

Fig. 2. Inner view of crushed head showing frontals, parietals, intertemporals, supratemporals and various cheek plates.

Fig. 3. Impression of the inner surface of the roofing bones, showing well the shape of the interfrontal bone.

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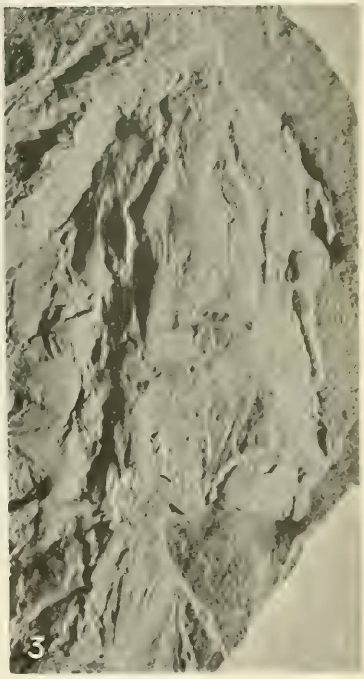
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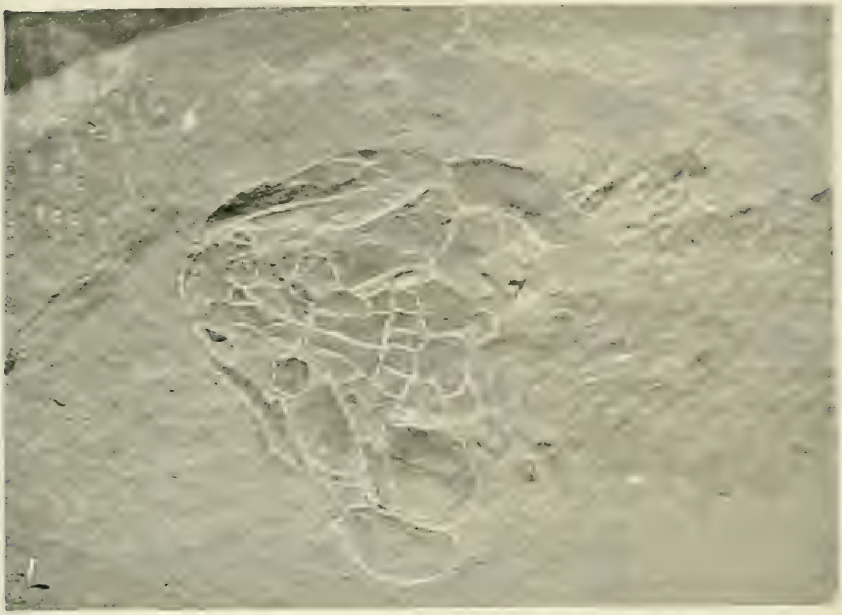
PLATE 6.

Fig. 1. *Osteolepis Macrolepidotus,* Agassiz. Top view of crushed head showing also the scaled lobe of the right pectoral fin.

Fig. 2. *Eusthenopteron Foordi,* Whiteaves. Principal gulars showing area of over-lap of medial gular.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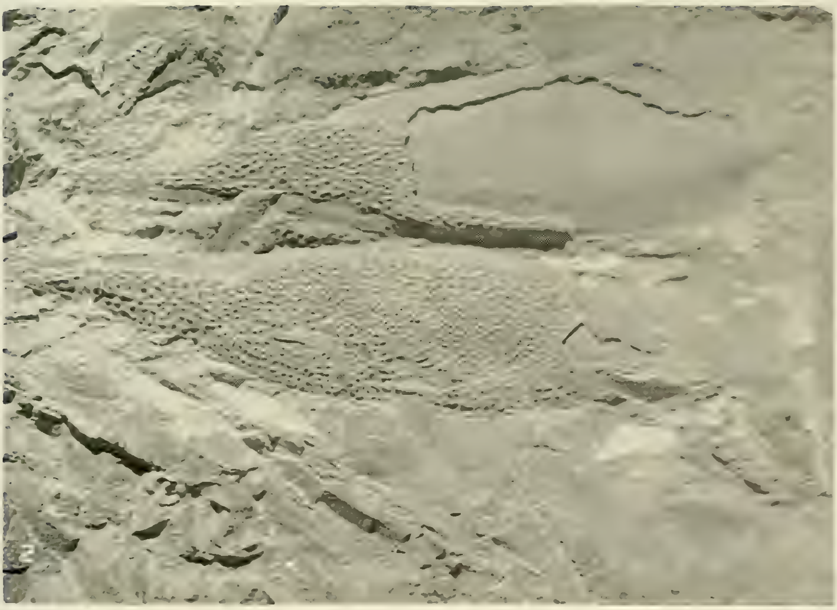
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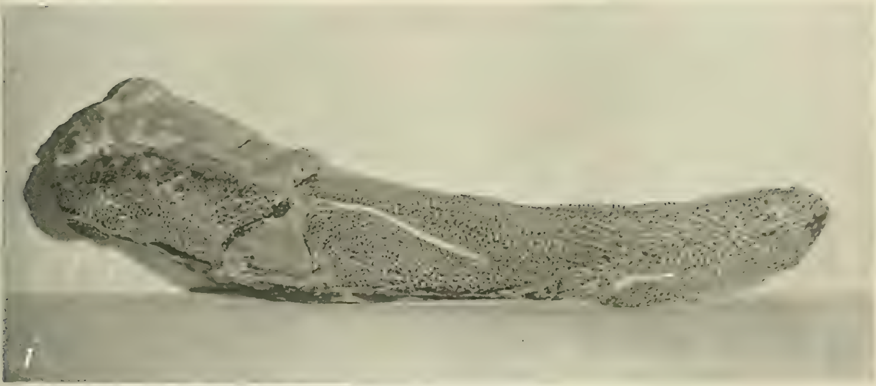
PLATE 7.

Eusthenopteron Foordi, Whiteaves.

Fig. 1. Right mandible in outer view. Sensory canals outlined in Chinese white.

Fig 2. Inner view of the same.

Fig. 3. Horizontal section through maxilla and ectopterygoid showing teeth in position.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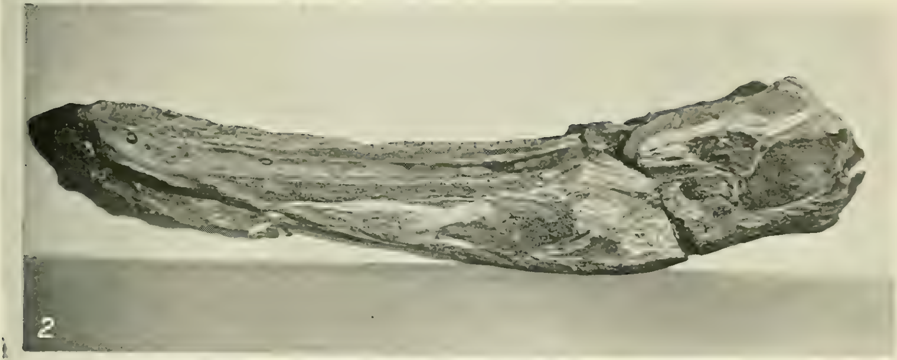
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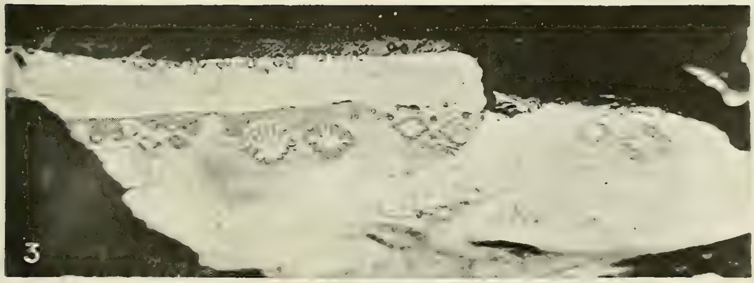
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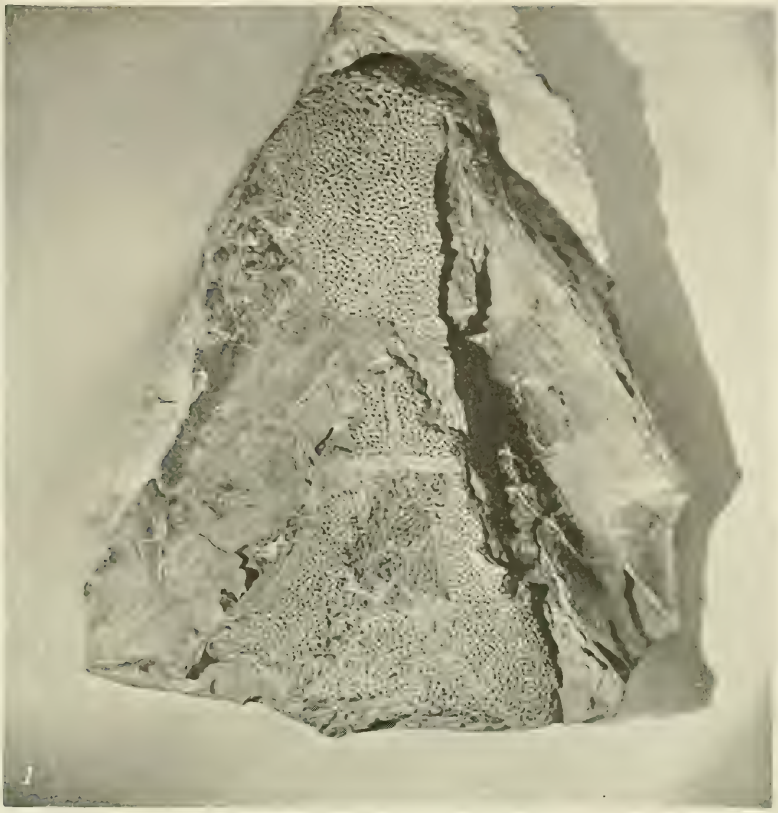
PLATE 8.

Eusthenopteron Foordi, Whiteaves.

Fig. 1. Head, part of the roofing bones broken away so as to reveal the pterygoids.

Fig. 2. Side view of right metapterygoid, entopterygoid, ectopterygoid and palatine.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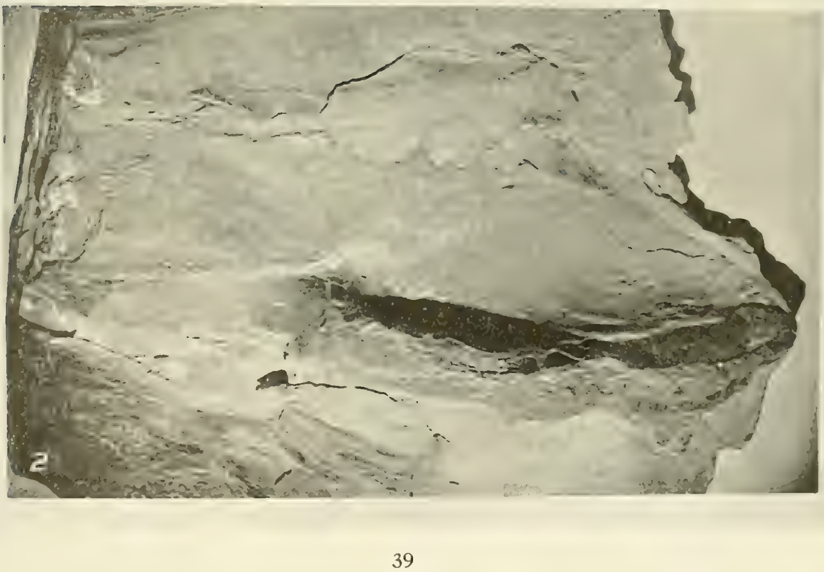
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PLATE 9.

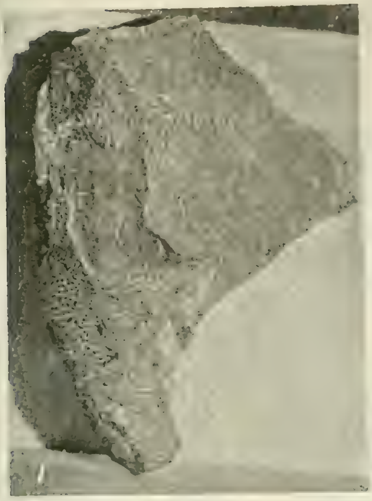
Eusthenopteron Foordi, Whiteaves.

Fig. 1. Interfrontal and right frontal, to show relations of roofing bones, with internal elements illustrated in next figure.

Fig. 2. Side view of the specimen seen in fig. 1 showing parasphenoid and interorbital septum with foramina.

Fig. 3. Inner bones of the cranium in side view showing prootic, parasphenoid, interorbital septum with foramina and olfactory chamber.

Fig. 4. Left side of same cranium as fig. 3, showing top of interorbital septum, with forward end of brain case; together with pterygoid and palatine bones in lateral view.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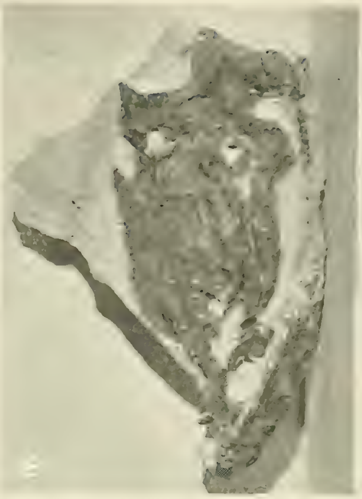
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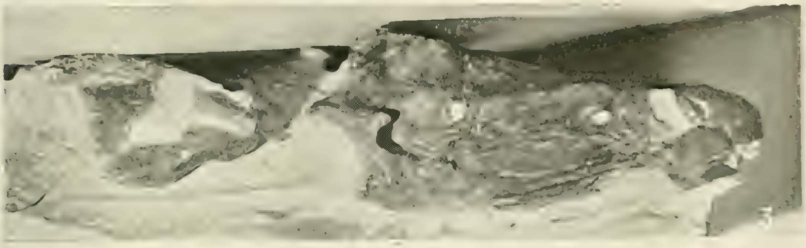
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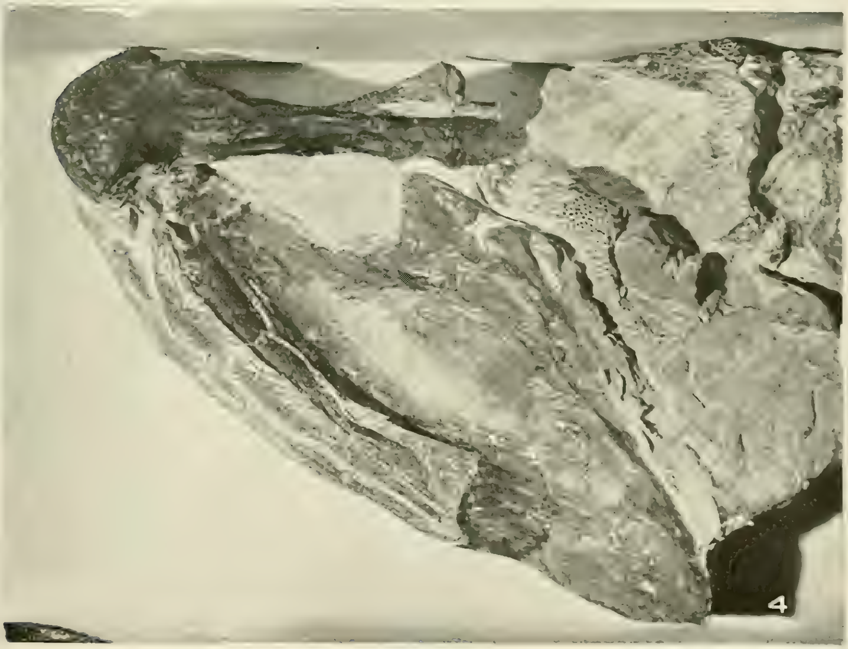
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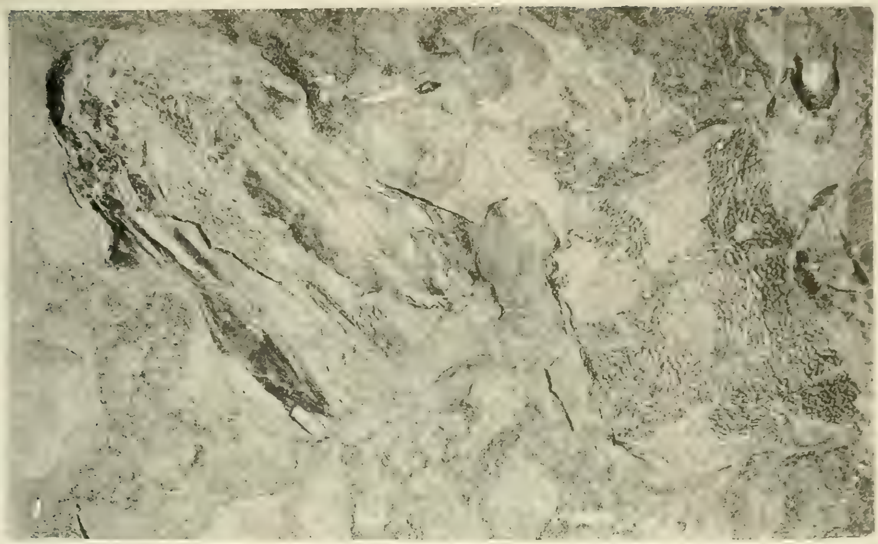
PLATE 10.

Eusthenopteron Foordi, Whiteaves.

Fig. 1. Specimen showing head from above; the parietals detached. Frontal portion of this specimen is figured in oral view below.

Fig. 2. Enlarged view of the underside of the same specimen showing premaxilla, parasphenoid and vomers, the latter containing a tusk and a pit for the successional tusk.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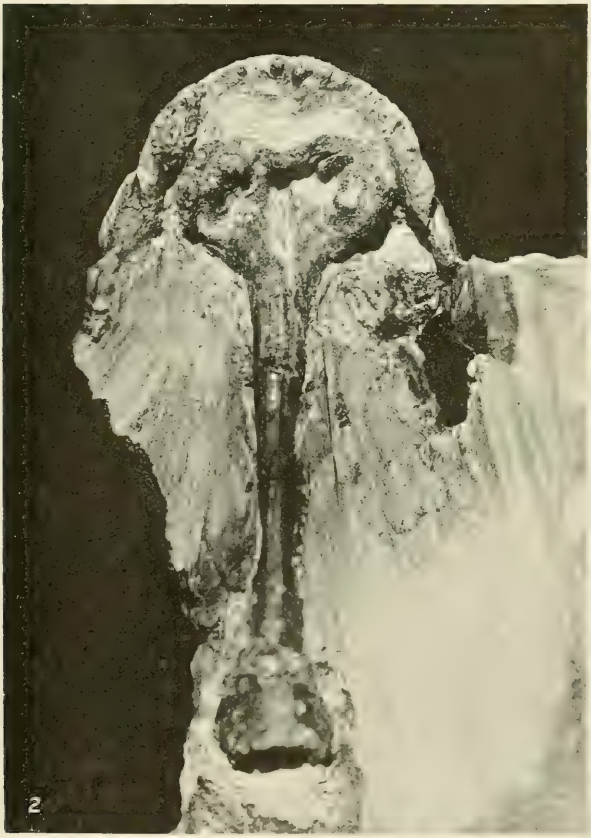
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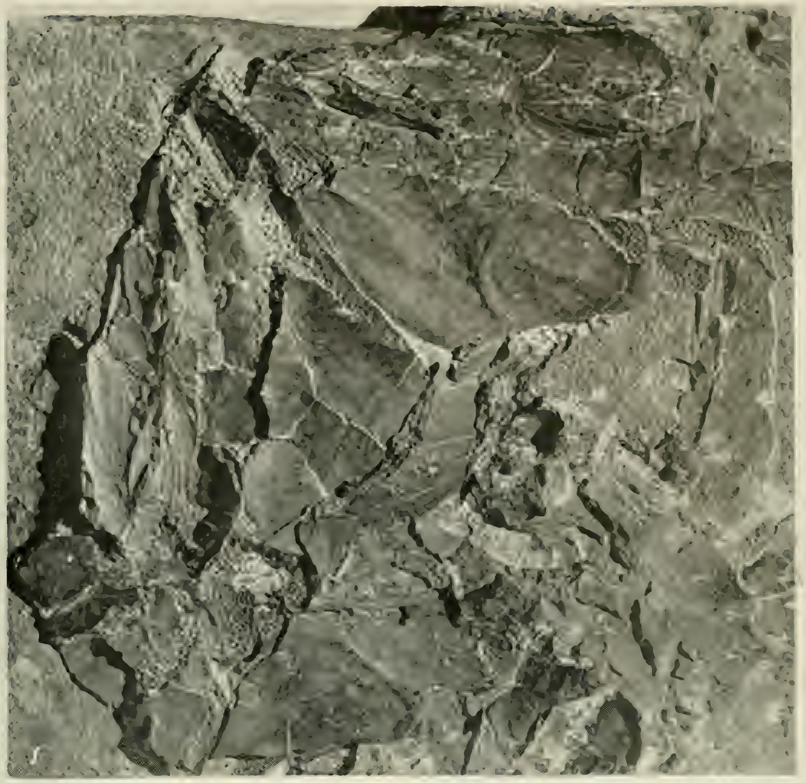
PLATE 11.

Fig. 1. *Holoptychius Quebecensis,* Whiteaves. Inner view of gular plates and fragmentary mandibles.

Fig. 2. *Eusthenopteron Foordi,* Whiteaves. The left pectoral fin with its supports and showing scaled lobe and fin-rays ornamented with tubercules.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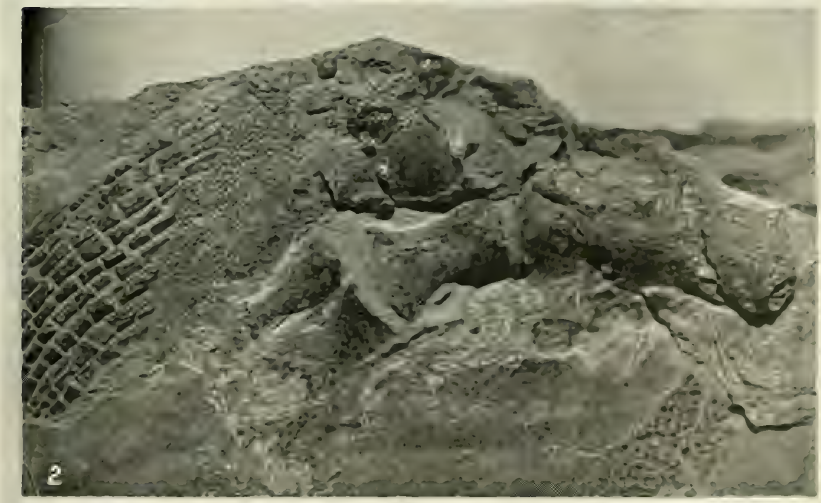
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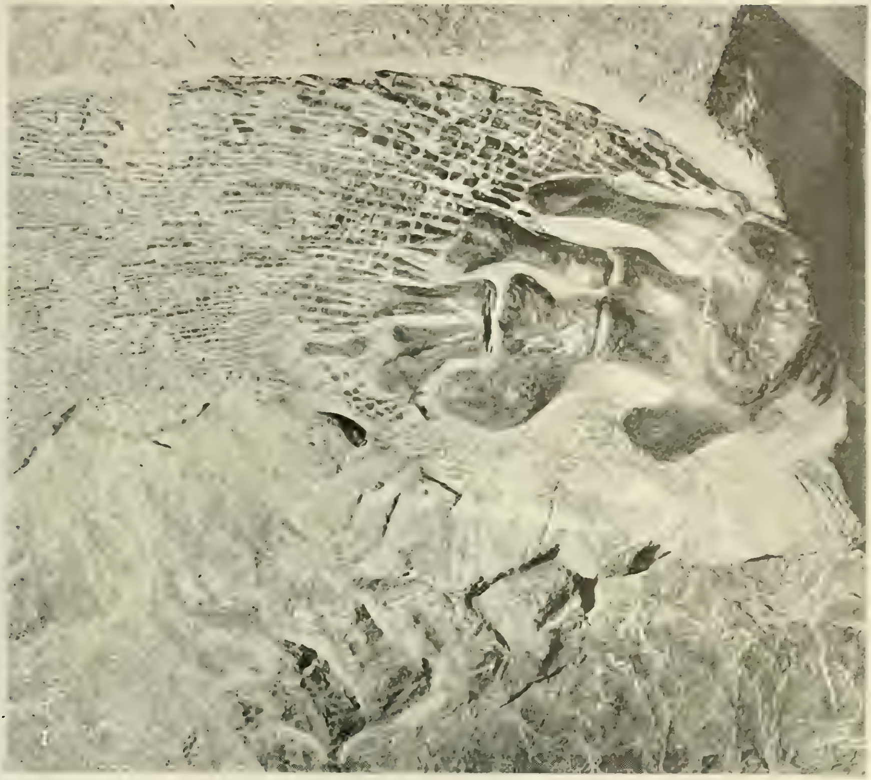
PLATE 12.

Eusthenopteron Foordi, Whiteaves.

Fig. 1. Left pectoral fin with its supports, the limb of the proximal segment having been destroyed in developing the specimen is restored in plaster.

Fig. 2. Skeleton of the caudal portion showing neural and haemal spines, radials and supports of the second dorsal and anal fins.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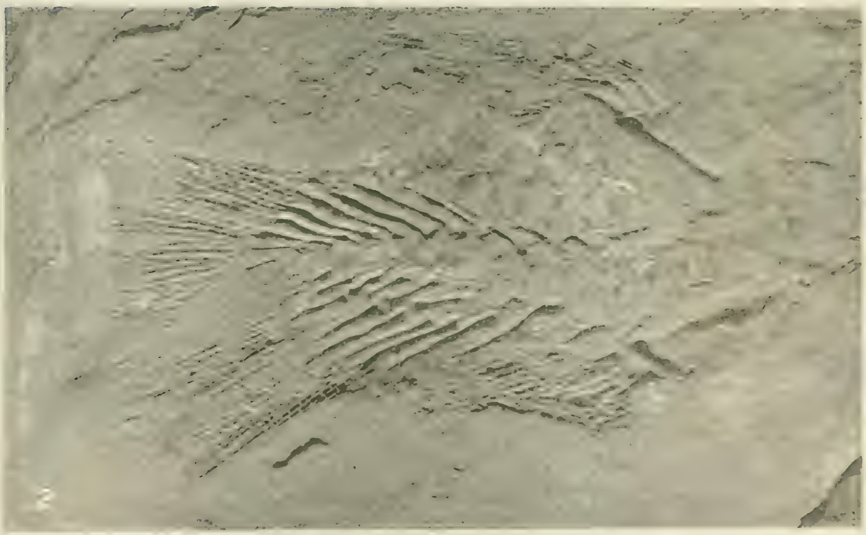
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PLATE 13.

Eusthenopteron Foordi, Whiteaves.

Supports of the ventral fins showing also, apparently, the position of the vent.

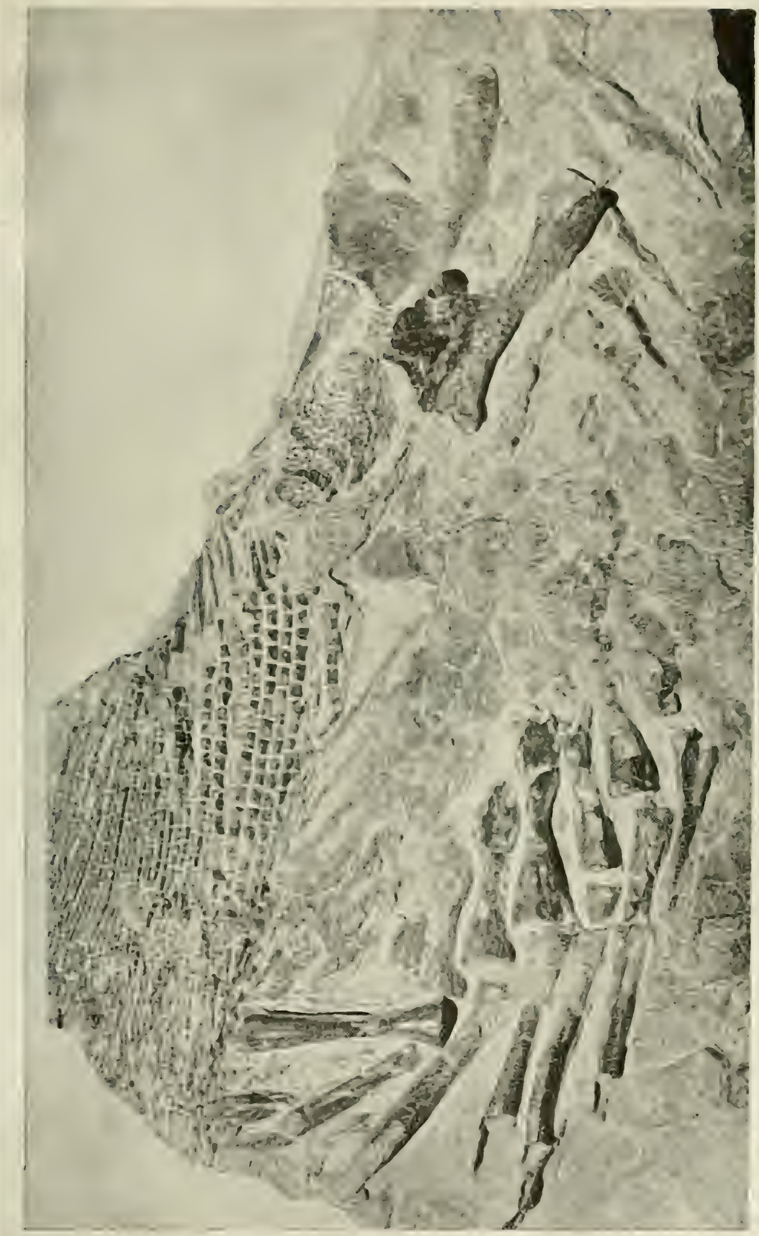


PLATE 14.

Eusthenopteron Foordi, Whiteaves.

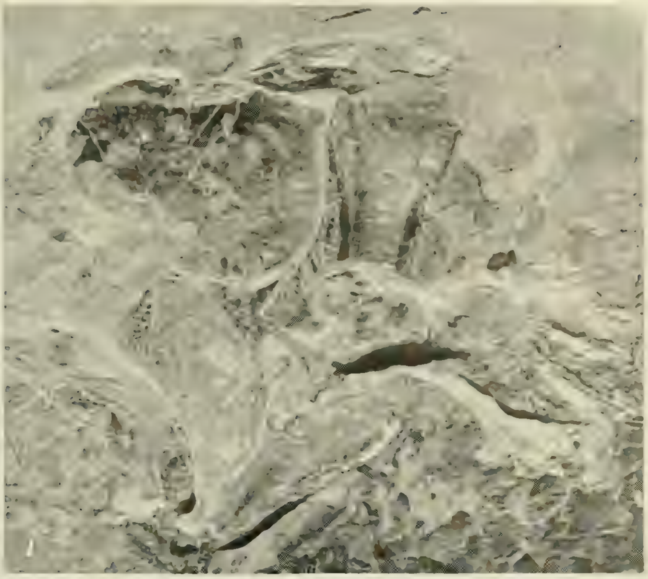
Fig. 1. Inner view of right pectoral girdle showing the scapulocoracoid element in place.

Fig. 2. Parietal region from above showing ex-occipitals.

Fig 3. Same specimen seen from behind.

Fig. 4. Same specimen seen from below showing brain case.

Fig 5. Same specimen in side view (right).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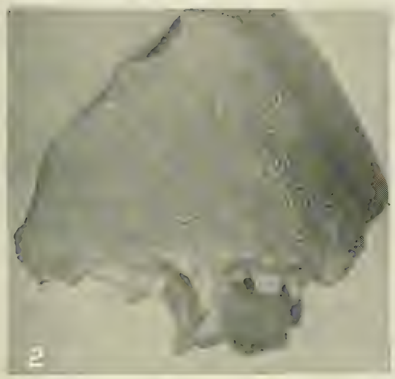
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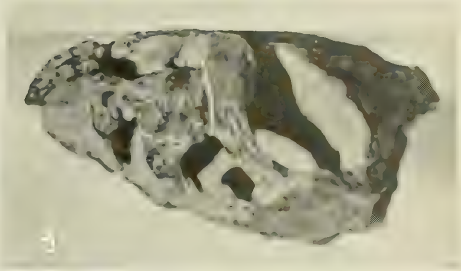
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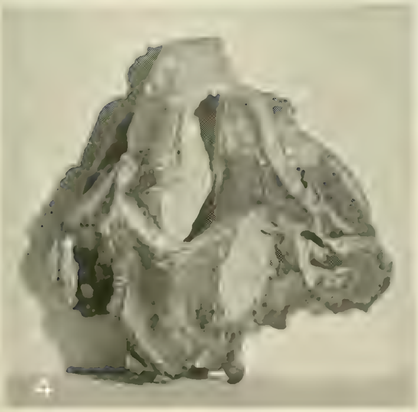
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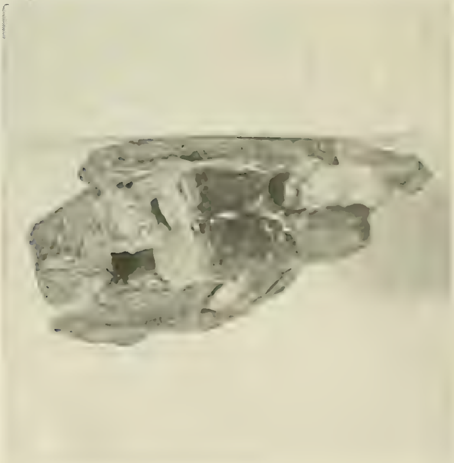
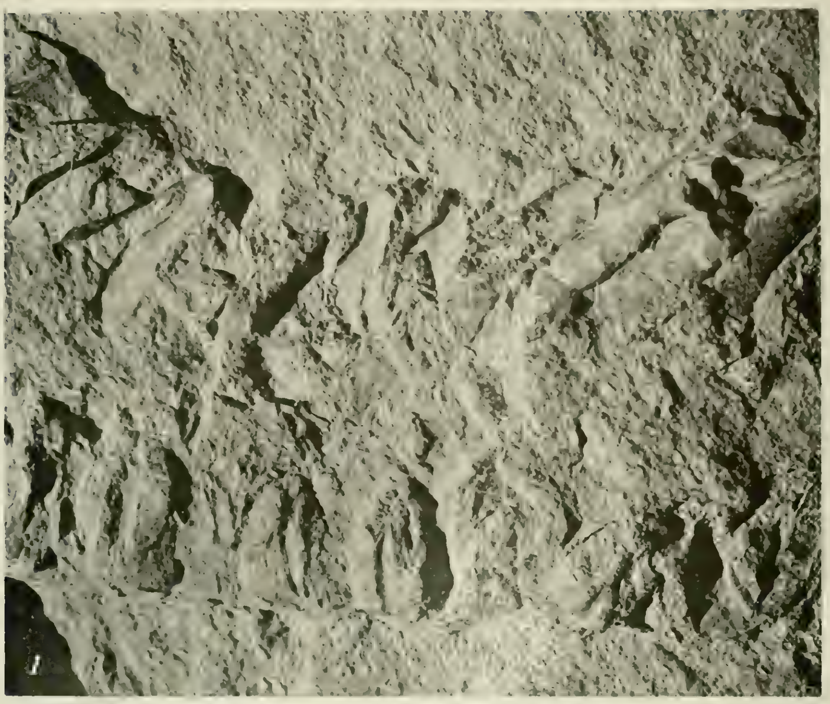


PLATE 15.

Eusthenopteron Foordi, Whiteaves.

Figs. 1 and 2. Vertebral centra and neural spines.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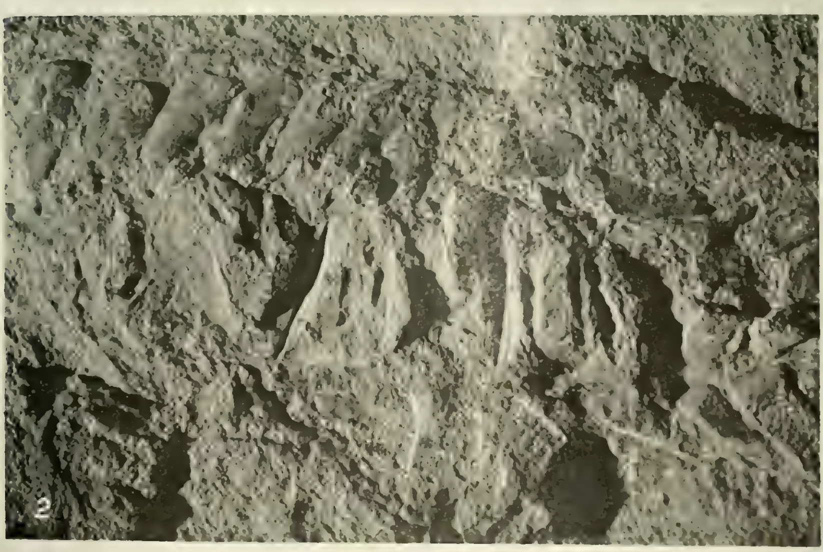
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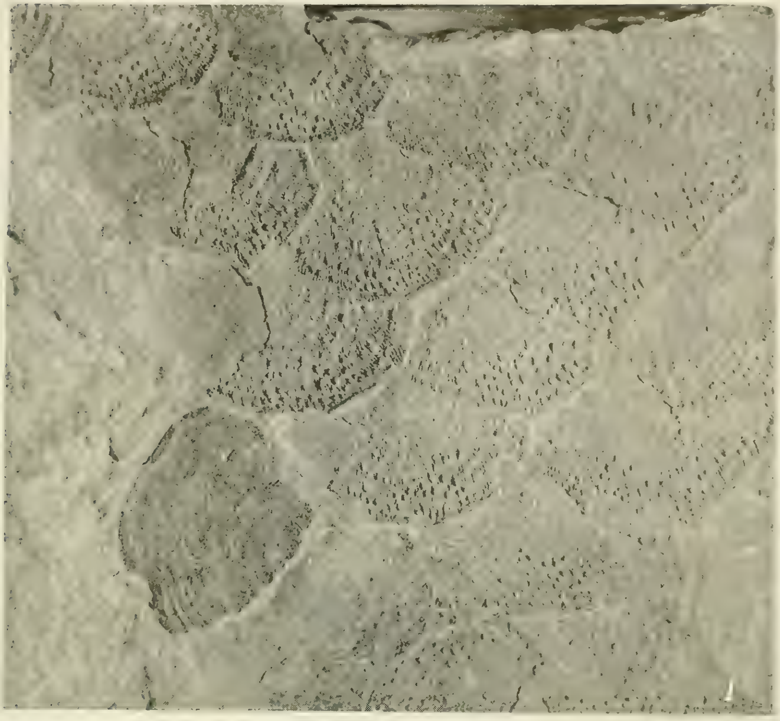
PLATE 16.

Fig 1. *Eusthenopteron Foordi,* Whiteaves. Scales of large individual showing ornamentation.

Fig. 2. *Holoptychius Quebecensis,* Whiteaves. Clavicle and scales showing ornamentation.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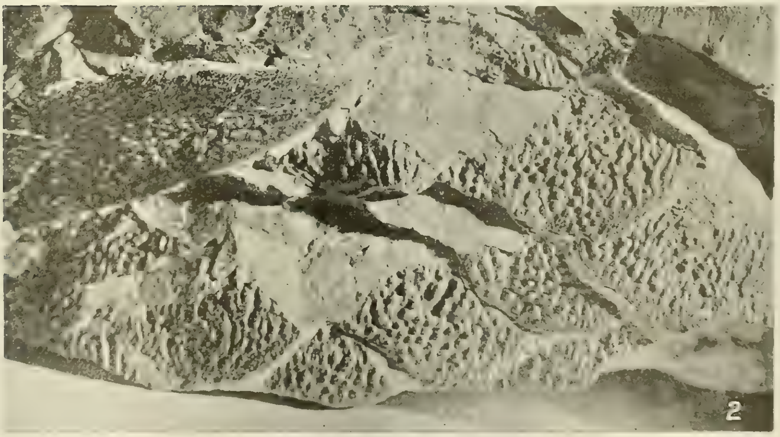
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PLATE 17.

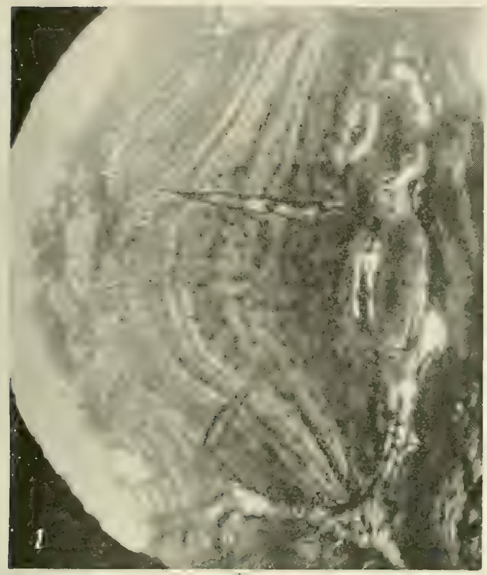
Eusthenopteron Foordi, Whiteaves.

Fig. 1. Micro-section of head plate.

Fig. 2. Cross-section taken near tip of tooth. (Highly magnified.)

Fig. 3 Cross-section of a portion of tooth taken midway between tip and base. (Highly magnified.)

Fig. 4. Cross-section of the base of tooth showing complex infolding of its walls. (Highly magnified.)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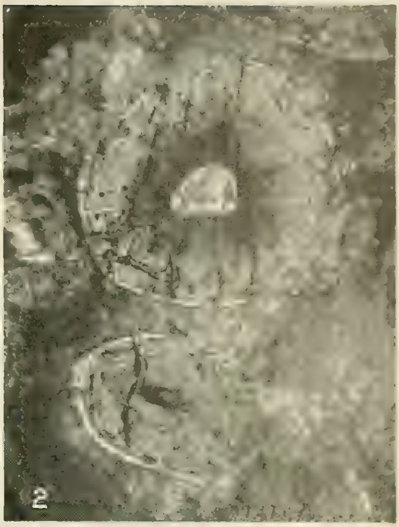
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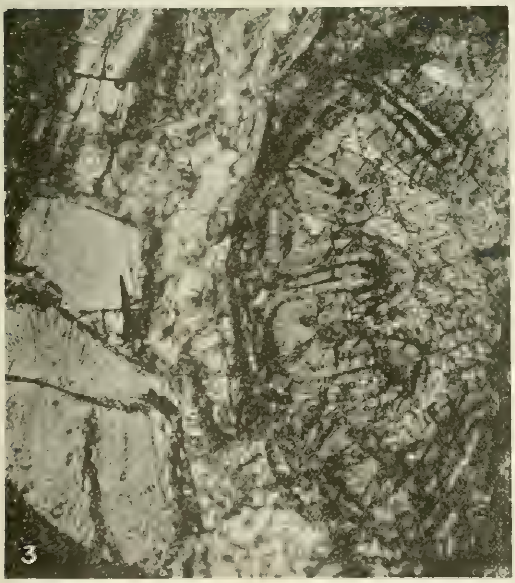
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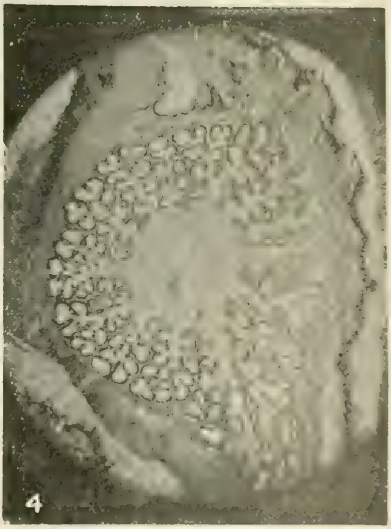
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PLATE 18.

Fig. 1. *Eusthenopteron Foordi,* Whiteaves. Micro-section of head plate.

Fig. 2. *Eusthenopteron Foordi,* Whiteaves. Micro-section of upper portion of scale.

Fig. 3. *Holoptychius Quebecensis,* Whiteaves. Longitudinal section of scale near its termination.

Fig. 4. *Holoptychius Quebecensis,* Whiteaves. Longitudinal section through parts of three scales.

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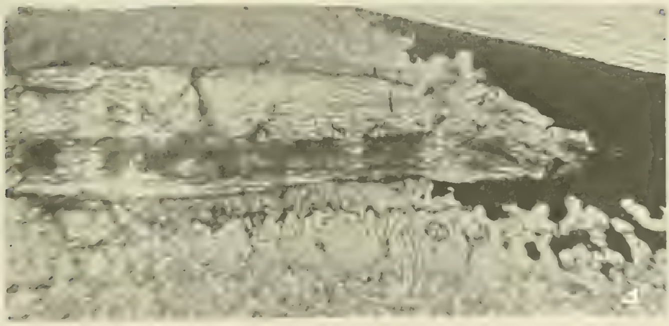
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With the compliments of the author.
William L. Bryant

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The Genesee Conodonts

With Descriptions of New Species

BY

WILLIAM L. BRYANT

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THE GENESEE CONODONTS

BY WILLIAM L. BRYANT

Conodonts are the teeth of some unknown family of animals formerly inhabiting the ancient seas of Europe and America. They range in geologic time from the Silurian to the lower Carboniferous.

The teeth are very small, rarely exceeding a millimeter in length and perceptible to the unaided eye only as minute black or horn-colored objects with a resinous lustre. When weathered by acidic agents they lose their color, and white Conodonts are often conspicuous upon black shales, indicating the presence of sulphuric acid consequent upon the decomposition of pyrite. They are composed of carbonate and phosphate of lime.

There is a great variety of form among the Conodonts. Simple and compound laniary teeth are found in the more ancient rocks, while in upper Devonian times a grinding dentition was introduced, bearing mute witness to the struggle for existence of these creatures as the conditions of life became more difficult. In their latter days they may also have acquired a dermal defensive armor as indicated by certain remains in the Conodont bed of Eighteen Mile Creek.

Aside from the speculative interest concerning the zoological affinities of these minute fossils, they may have an important geological value as time indices. Many of the rocks in which they are found are almost destitute of other fossils, and one need only recall the long controversy over the age of the Ohio and Kentucky Shales—both Conodont bearing formations—to realize the need for a study of the evolution of these teeth and more complete descriptions of the varieties which occur in rocks of

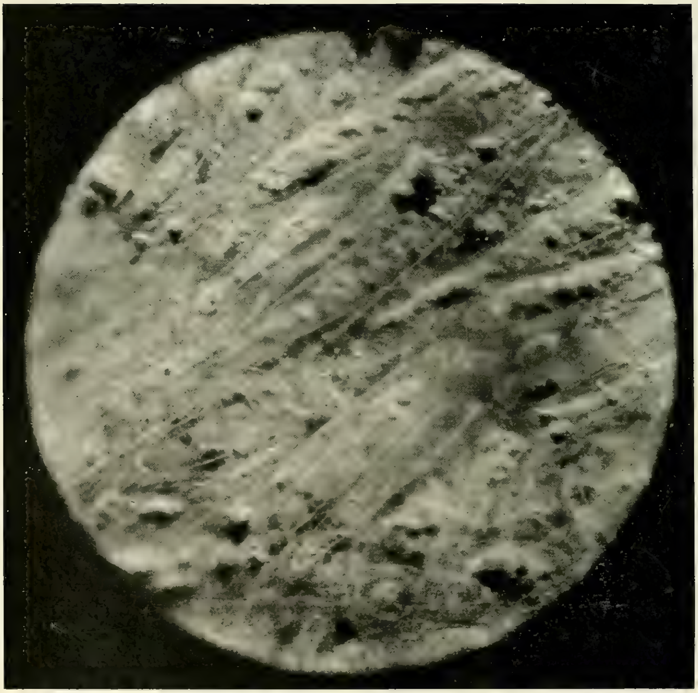

Fig. 1. Weathered surface of Genundewah limestone, magnified to show the Styliola shells of which it is composed.

successive ages. It was partly for this purpose that I undertook a re-study of the forms occurring in the Conodont bed of the Genundewah Limestone, a rock well known to be of Genesee age.

Before proceeding further it is advisable to discuss briefly the nature of the rock in which the specimens described in this paper have been found. The Genundewah limestone emerges from the bed of Eighteen Mile Creek in Erie County at the railroad bridge rather more than a mile from the mouth of the stream. It here constitutes the base of the Genesee group and consists of two closely opposed strata, sometimes separated by a thin layer of shale, sometimes merging into each other and having a maximum thickness of more than two feet.[1] The upper member was formerly known as the Styliola limestone, and is a hard, dense rock consisting almost entirely of the minute shells of Styliola fissurella closely meshed together, although Conodonts and plant and fish remains are not uncommon. Fig. 1 is a photomicrograph of the weathered surface of the rock showing the closely packed shells.

This interesting limestone was first fully described by Dr. John M. Clarke[2] and in line with his deep water theory of the origin of the succeeding black shales, he has more than once referred to this rock as a typical Pteropod ooze.[3]

In modern seas Pteropod ooze ranges from 400 to 1,700 fathoms,[4] a greater depth than most geologists would be disposed to assign to the deposits of the epi-continental ancient seas[5] and in this connection it should not be forgotten that Dr. Paul Penseneer[1] has denied that the Devonian Styliola has any affinities with straight shelled Pteropods, which he claims are specialized forms derived from coiled ancestors and first appear in the Tertiary. Later authorities, however, do not accept this conclusion.

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[1] Not four to six inches as stated by Houghton, Bulletin Buffalo Society of Natural Sciences, Vol. XI, p. 34.

[2] On the Higher Devonian Faunas of Ontario County, N. Y., U. S. Geological Survey Bulletin 16, p. 14.

[3] It is, however, more homogenous than the modern Pteropod ooze owing to the absence of Heteropods, etc.

[4] Sir John Murray. The Depth of the Ocean, p. 169.

[5] "I have busied myself much with recent deep sea sediments, have studied those of the Challenger Expedition and in my geological studies have considered again and again whether anywhere a fossil rock possesses abyssal characteristics, and can state that nowhere have I met with a rock either from Palaeozoic or Mesozoic deposits that by its structure and nature of deposition corresponds to the present sediments of the deep sea."—Dr. Johannes Walther, American Journal of Science, 4th Series, Vol. XXXI, p. 60.

The lower member, an impure phosphatic and fragmental limestone, named many years ago by Hinde "the Conodont bed," attains a maximum thickness of four or five inches at the point of emergence from the creek bed and apparently thins out in every direction. Wherever it has been found out-cropping in other localities in the vicinity it apparently occurs only in thin patches or lenticular layers. The rock is in fact the remains of an ancient sandbar and is composed of water-worn quartz grains, Crinoid stems and other fragmental material; with pyrite, a very few invertebrates, an enormous number of Conodonts and the osseous plates and teeth of fishes.

On turning over a slab of this rock, its sandbar nature is well shown. The heavier material has worked to the bottom, and there in relief are to be seen Crinoid stems, water-worn pebbles sometimes two inches in diameter; together with the disarticulated remains of arthrodires, the teeth of sharks and ganoids and occasional fragments of driftwood. One such slab collected by the writer measures only 11″ x 18″ and yet contains the remains of eight species of fishes together with numerous water-worn pebbles. All this, together with the great quantity of rhizocarps in the thin shale coating the surface of the beds and sometimes included within them, indicates shallow water conditions with land in the near vicinity. Some of the rock shows evidence of cross-bedding.

The variety of fish remains contained in the Conodont bed is remarkable, the writer having collected from one small exposure bones, teeth and spines representing twenty-seven genera and forty species. It is thus one of the richest and most interesting storehouses of ancient vertebrate life to be found anywhere in the world. Fig. 2 is a photograph showing the Genundewah limestone and Conodont bed in Eighteen Mile Creek. Underneath is seen the Moscow shale with its concretionary layer.

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[1] Report on the Pteropods. Voyage of H. M. S. Challenger, Zoology, Vol. XXIII.

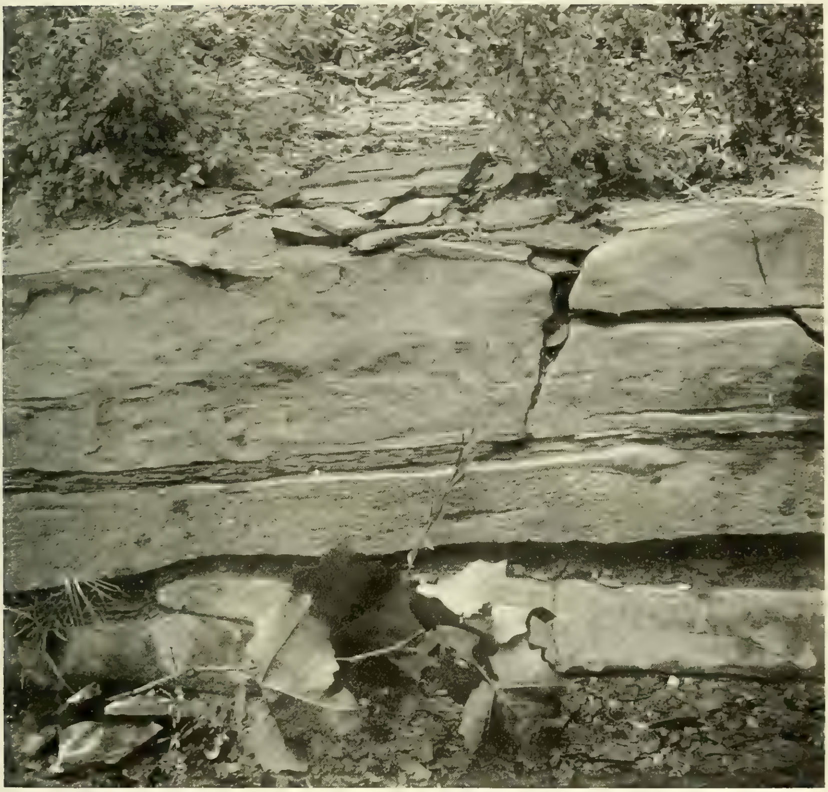

Photo by Houghton.

Fig. 2. The Genundewah limestone and Conodont bed at Eighteen Mile Creek, N. Y. Underneath is the concretionary layer of the Moscow shale.

Ever since the first discovery of these fossils in 1856 by Doctor Christian Pander in the lower Silurian rocks near Petrograd, Russia, there has been much speculation as to their zoological affinities. Dr. Pander himself believed them to be the teeth of sharks, in which view he was supported by Louis Agassiz.

In the second volume of the Palaeontology of Ohio, Dr. J. S. Newberry, at that time the foremost American authority on fossil fishes, figured a number of Conodonts from the Cleveland shales under the provisional head of Marsipiobranchii; and in discussing their relationship he quoted Prof. E. S. Morse and William Stimpson as of the opinion that they might belong to the progenitors of our living forms of mollusks, particularly the Nudibranches.[1]

Dr. Newberry suggested that these objects might be the teeth of Cyclostomous fishes and compared them with the teeth of Myxine and Bdellostoma. Prof. Huxley, to whom Dr. Hinde showed examples of Conodonts, concurred in this opinion. However, in 1889[2] Dr. Newberry adopted the current Annelid hypothesis saying that probably no one now believes that they are the teeth of fishes.

The next discovery of Conodonts in America was that by Dr. George J. Hinde[3] who found them in the Chazy rocks on the Ottawa River; in the Cincinnati group near Toronto; in the Genesee and Portage shales near Buffalo, as well as in the Huron shales of Lambton County, Ontario, and of Kentucky. Dr. Hinde discovered and named the Conodont bed at Eighteen Mile Creek, referring it to the upper Hamilton but it is now known to be of Genesee age. In his paper he figured and described one new genus and thirty-five species, mostly new. Owing to the difficulty of extracting his specimens from the matrix and their curiously twisted shapes he unfortunately, in several instances, described as separate species the upper and inferior surfaces of the same form. His new genus was erected to receive teeth of various forms, some of which apparently belonged in various genera established by Pander, and which, from the circumstance of their having been found associated together on a slab of shale, Dr. Hinde assumed to belong to one individual. This assumption, however, does not take into consideration the possibility that the deposit may have been the ejecta of fishes, and leads to confusion in the classification.

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[1] In 1912 the writer showed some of the more complex dental plates from the Conodont bed to Prof. Morse who said he did not believe they were the teeth of worms or mollusks, and thought they must belong to fishes.

[2] U. S. Geological Survey, Monograph XVI.

[3] "On Conodonts from the Chazy and Cincinnati Groups of the Cambro-Silurian and from the Hamilton and Genesee Shale Divisions of the Devonian, in Canada and the United States." Quarterly Journal, Geological Society, Vol. XXXV, p. 351, 1879.

Professor Owen in the second edition of his "Palaeontology" had expressed the opinion that Conodonts have most analogy with the spines, or hooklets, or denticles of naked Mollusks or Annelids. Dr. Hinde in dissenting says: "In the Cambro-Silurian rocks the fossils of marine invertebrates are very varied and abundant but there are no large Gastropods whose lingual teeth could be supposed to be similar to Conodonts, nor the carapaces and segments of any Crustaceans to which they could have been attached as defensive spines. In the Devonian strata where the Conodonts are much more numerous and diversified in form than in the lower rocks, the only invertebrate fossils accompanying them are Crinoids and Brachyopods; but there are here plenty of fragments of undisputed fish teeth and bones. That, however, the Conodonts cannot be referred to the horny jaws of Annelids may be conclusively shown by the discovery by the writer of these Annelidan structures in the same strata with Conodonts, from which the former can be readily distinguished by their chemical composition and their resemblance to the jaws of existing Annelids."

Dr. Hinde reasons against the probability of Conodonts having been the teeth of naked Mollusks and concludes by referring them provisionally to some low type of fishes similar to the existing Myxinoids. As to the microscopic structure, he corroborates the results obtained by Pander. "I can detect the same delicate conical lamellar structure both in the specimens from the Chazy and in some of those from the Devonian; in other Devonian specimens, however, the basal portion appears to be homogenous and without structure, whilst the teeth imbedded in this base have either a clouded fibrous appearance, or seem to be composed of minute nuclei, as represented by Pander (Monog. tab 20, Figs. 11, 12)."

Seven years later Doctors von Zittel and Rohon published a paper on Conodonts[1] in which they reviewed the literature of the subject, and concluded, from a comparative study of their microscopic anatomy, that the Conodonts have nothing structurally in common with the dentine or horny teeth of fishes, horny teeth of Cyclostomes, lingual teeth of Mollusks, hooklets of the Cephalopoda or segment spines of Crustacea, but that they agree in form and structure with the masticatory apparatus of the Annelida and Gephyrea.

The following year some new American localities were recorded by Dr. J. M. Clarke[2] who accepts the conclusions of Zittel and Rohon, and figures more than twenty Conodonts from the Naples shales of Ontario County, N. Y. Following Hinde, he figures as Polygnathus dubius a profile view, and as Polygnathus pennatus the upper aspect of the same plate.

Since the publication of Zittel and Rohon's paper most authors have accepted their conclusions. Zittel himself, however, in his Text-book of Palaeontology, admits that the true position of Conodonts cannot yet be said to be satisfactorily determined, and S. A. Miller[3] has latterly declared that he is firmly convinced that the Conodonts are not the teeth of Annelids but belong to the masticatory apparatus of Crustaceans. He omits to give his reasons for this decision.

In 1894 Jaroslaw Perner described as Prioniodus barrandei a new Conodont from the Silurian of Bohemia. He omitted any discussion of the zoological affinities of Conodonts.

Ray S. Bassler, Curator of Palaeontology of the U. S. National Museum, in his recently published index of American Ordovician and Silurian fossils[4] has placed the Conodonts tentatively as fish plates and teeth under the class Pisces.

And thus the present state of our knowledge of the subject may be summarized in the words of Dr. Arthur Smith Woodward:[1] "Their histological structure is so different from that of any teeth known that their affinities are quite undeterminable. They are apparently formed of structureless concentric lamellae without any trace of vascular canals or capillaries and the substance of the fossils is chiefly carbonate of lime. Some Conodonts consist only of a single cusp; others of a series of cusps upon one base; and minute plates, ornamented on one side with tubercles are sometimes found in association with them. They may even be the teeth of unknown Nudibranches or Annelids or the hooks of Cephalopods, and can thus be dismissed as fragments too inconclusive for consideration here" (as the teeth of vertebrates).

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[1] Ueber Conodonten: Sitzungber. d. k. bayr. Akad. d. Wiss. Mathem-phys. Classe, p. 108, 1886.

[2] Annelid Teeth from the Lower Portion of the Hamilton Group and from the Naples Shales of Ontario County, N. Y. Sixth Annual Report of the State Geologist. Albany, 1887.

[3] North American Geology and Palaeontology. Second Appendix, 1897.

[4] Bibliographic Index of American Ordovician and Silurian Fossils. Bulletin 92, U. S. National Museum, 1915.

It is true that in form and in certain details of internal structure, Conodont denticles recall conditions in the teeth of recent Annelids. Thus in the modern Nercis,[2] the inner portion of the tooth is darkened by a black pigment. This is also the case with certain Conodonts, as for example, that shown on Plate III, fig. 8, where a vertical view of three broken denticles exhibits the same pigmented interior.

Zittel and Rohon[3] list a number of forms of Conodonts resembling the teeth of various recent Annelids; and there is a very striking similarity between the tooth of Halicryptus figured by them and the Conodont illustrated on my Plate III, fig. 10.

Fractured surfaces of Conodonts, like the cleavage planes of crystals, have the same lustre as the normal exterior.

I figure on Plates XII, XIII and XIV certain fragmentary ornamented plates which may have formed the defensive covering of these mysterious animals. The plates are always broken, rarely exhibiting a natural contour. They, like the Conodonts, are composed of structureless carbonate and phosphate of lime[4] and have the same fine, polished submetallic or resinous lustre. The upper surface is sculptured with curved and subparallel raised lines, or grooves, but in one species the lines meander, forming a reticulated ornamentation.

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[1] Vertebrate Palaeontology for Students of Zoology. Cambridge, 1898.

[2] Compare Rohon and Zittel, Loc. cit., Plate II, fig. 9.

[3] Loc. cit., p. 131.

[4] They give with the molybdate of ammonia test a very strong phosphatic reaction.

These plates are not liable to be confused with the shells of Brachyopods or the scales or plates of ganoid fishes which occur in the same rock. They are quite flat and the thinner ones are translucent. They have not been noticed from other Conodont bearing localities but it is possible that their presence has been overlooked. I have figured all the forms that occur in the Conodont bed and, if they pertain to Conodonts, these few perhaps represent all or nearly all of the species possessing the great diversity of teeth illustrated in the following pages. The under surface of one of the plates is shown in fig. 3 on Plate XIV. Some of them resemble, at least in ornamentation, fragments of Lingula valves.

The presence of these sculptured plates in association with the Conodonts would seem to throw doubt upon the hypothesis of the Annelid origin of these fossils. It is true that certain Annelids (Lepidonotus, Polynoe) are defended by a double series of broad dorsal scales, but these are thin chitinous structures quite different from the calcareous fossil plates. On the whole, the longer I have studied these organisms, the more have I become convinced that the true Conodonts have hardly anything really diagnostic in common with Annelid jaws. If, as I shall hereinafter try to demonstrate, certain of the leaf-like forms are of the nature of pavement teeth, then the conclusion seems almost unavoidable that the Conodonts must be considered as the dentition of some primitive type of fishes. It is to be hoped that some day the fortunate discovery of the teeth and plates in well-preserved natural association will settle the question of the affinities of these perplexing structures.

The possible value of Conodonts as index fossils has recently been remarked by Dr. Edward Kindle.[1] "These fossils have long been known in the Ohio Shale," writes Dr. Kindle, "but with the exception of a very few species have remained undetermined and undescribed. When they have been described and the species which are confined to the upper and lower horizons of the shale distinguished, they will prove to be an invaluable aid in correlating the different parts of the Ohio Shales with their equivalents in the Chattanooga Shale in Kentucky and farther south."

In searching for study material the writer was fortunate enough to discover a thin layer of decomposed rock adhering to the under surface of the Conodont bed. This was subjected to repeated washings and boiled with the addition of washing soda, and the resulting sand was found to be exceedingly rich in Conodonts, they making up nearly one-half of the mass. Although much of the material was broken, beautifully preserved examples were plentiful and these were picked out, transferred to slides and mounted so as to exhibit the superior, inferior and profile aspects of a series of all the forms herein illustrated.

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[1] Unconformity at the Base of the Chattanooga Shale in Kentucky. American Journal of Science, Vol. XXXIII, p. 128.

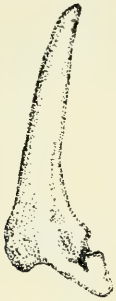

Fig. 3. Prioniodus recedens, Bryant. × 25.

PRIONIODUS RECEDENS, Spec. Nov.

Text fig. 3. Plate I, figs. 1-2, 6-14; Plate II, figs. 1-4, 7, 9.

It is clear that any attempt to classify these obscure fossils will have more palaeontological than zoological value. The simplest form from the Conodont bed consists of a single robust, curved and blunted tooth, nearly circular in cross section, arising from a somewhat expanded, hollow base.

The cavity beneath the base is lined with smooth polished walls and apparently extends but a short distance upwards into the tooth. Plate III, fig 7, shows a thin section of a related species, cut so as to bisect this cavity, but not illuminated to show the lamellar structure of the tooth. The base is convex on one side and concave on the other and from this fact it is easy to determine that these teeth must have been symmetrically arranged in pairs, as both rights and lefts are to be seen on Plate I.

Were some of these teeth to be found isolated, one would place them in Pander's genus, Drepanodus; but when one examines a series, it is at once apparent that they merge insensibly into other forms. The base gradually lengthens into a narrow arch upon which is supported, on either side of the main cusp, a row of smaller, blunted denticles. These denticles vary in number with the growth of the base and their quantity seems to result from what Professor Owen used to term a vegetative repetition of parts.

The form, character and microscopic structure of these teeth are such as to recall somewhat the description and figures given by Pander of Prioniodus tulensis, a species hitherto recorded only from Russia. Prioniodus recedens, however, differs from Prioniodus tulensis in its more robust proportion, its less acute, tapering and recurved laniary tooth, its less sigmoidal profile, and in its subsidiary denticles, which are blunt and obtusely rounded. The base, too, is less compressed. It is clear, as above explained, that the number of subsidiary denticles is not a reliable character in defining species. I reproduce here (fig. 4) two of Pander's figures which show well the microscopic structure which obtains throughout the genus. The cavity under the main cusp in those examples which have an elongated base, is continued as a narrow, shallow and polished groove.

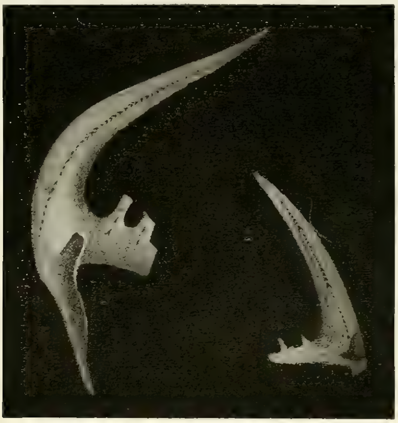

Fig. 4. Prioniodus tulensis, showing minute structure. After Pander.

PRIONIODUS ABBREVIATUS, HINDE[1]

Plate I, figs. 3-5; Plate III, fig. 7.

1879. Prioniodus abbreviatus, G. J. Hinde, Quar. Jour. Geol. Soc., Vol. XXXV, p. 359; Plate XV, fig. 15.

Dr. Hinde's description of this species, which he collected from the Conodont bed of Eighteen Mile Creek, is as follows: "Base of tooth very short and stout, at one end a comparatively long, nearly straight, cylindrical, blunted, main tooth, on one side of which are two blunted denticles with small knobs at their summits."

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[1] As Hinde's Paper is not always to be found in libraries, it may be remarked that rather poor copies of all his figures, together with brief descriptions, may be found in Prof. Grabau's work on the Geology and Palaeontology of Eighteen Mile Creek, Bull. Buffalo Soc. Nat. Sciences, Vol. VI, Part 2.

This species, like Prioniodus recedens, may have a variable number of subsidiary denticles, or none at all. I figure on Plate I, two of the latter kind. Figure 12 on the same plate which, however, probably represents a form of Prioniodus recedens, shows the knob-like denticles which, as Dr. Hinde says, are also characteristic of Prioniodus abbreviatus.

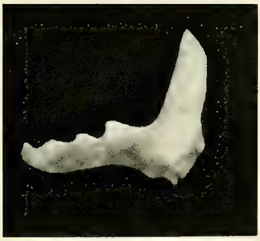


Fig. 5. Prioniodus hamatus, Bryant. × 25.

PRIONIODUS HAMATUS, Spec. Nov.

Text fig. 5. Plate II, figs. 5, 6, 8, 11.

Base narrow, slightly curved, and depressed at one end where it supports a large, robust and somewhat blunt tusk which is sometimes produced below the base. The outer margin of this tusk at its junction with the base usually bears a tubercule or short cusp. On the other side of the main tusk, the base carries four or five widely spaced denticles, variable in size and height. Base horn colored; teeth polished and tinted like ivory. Conodont bed, Eighteen Mile Creek.

PRIONIODUS ALATUS, HINDE

Plate III, fig. 10; Plate IV, figs. 1-7.

1879. Prioniodus alatus, G. J. Hinde, Quart. Journ. Geol. Soc., Vol. XXXV, p. 361; Plate XVI, fig. 5.

This is a larger form than Prioniodus recedens, but equally variable in the expansion of the base and in the number of denticles thereon supported. The main tooth is large, triangular and compressed, one side gently rounded, the other, with a more or less pronounced ridge extending from the base nearly to the apex. One arm of the arched base carries a series of denticles. The teeth are creamy white; the base horn-colored or blackish. Underneath the main cusp is a lozenge-shaped cavity. From this a narrow groove extends the length of the base.

Dr. Hinde was disposed to doubt the propriety of placing these teeth in Prioniodus, but Pander's definition is broad enough to include them. Like Prioniodus recedens, there are progressive forms varying from simple to compound teeth, and rights and lefts can be distinguished.

PRIONIODUS RADIATUS, HINDE

Plate IV, figs. 10-12; Plate V, figs. 1-5, 8; Plate VI, fig. 5; Plate VIII, figs. 1, 2, 4, 6, 8; Plate XIV, fig. 1.

1879. Polygnathus radiatus, G. J. Hinde, Quar. Jour. Geol. Soc., Vol. XXXV, p. 364, Plate XVI, fig. 20.

1879. Polygnathus dubius (in part), G. J. Hinde, Quar. Jour. Geol. Soc., Vol. XXXV, p. 362, Plate XVI, figs. 6 and 8.

1886. Polygnathus dubius (in part), J. M. Clarke, Report of State Geologist for 1885, Albany, N. Y., Plate A-1, fig 6.

This species is no less variable than the preceding form. The main tooth is always broad, slightly convex and inclined to the base; sometimes produced below it to form the walls of the lozenge-shaped cavity. The base is narrow, arched and bears on either side of the main cusp a row of denticles varying in size and often so closely crowded together that they seem to have interfered with each other's growth. The main cusp is also frequently constricted below and the whole appearance would suggest that the normal expansion of the base was prevented by the encroaching bases of adjoining plates. The flattened base often expands at either end.

As in other species these jaws or plates occur in pairs. They resemble in form the teeth from the Russian Devonian described as Ctenognathus verneuilli by Pander, and supposed by him to differ from Prioniodus in their cellular microscopic structure. The Genesee teeth, however, as shown rather obscurely by the photomicrograph of the thin section on Plate XIV, fig. 1, agree rather with Prioniodus in their internal laminations.

PRIONIODUS CLAVATUS, HINDE

Plate VI, figs. 3, 6.

1879. Prioniodus clavatus, G. J. Hinde, Quar. Jour. Geol. Soc., Vol. XXXV, p. 360, Plate XV, fig. 16.

This species is uncommon in the Conodont bed and it is difficult to find specimens which are not partly concealed by the matrix; while in the weathered and washed material the long, slender teeth are nearly always broken. The teeth are often more closely opposed than those shown in Dr. Hinde's figure. As many as seven or eight teeth are sometimes found on one side of the main cusp which is not so greatly differentiated from the others as in most species of the genus.

PRIONIODUS ERRATICUS, HINDE

Plate II, fig. 10; Plate VII, fig. 1.

1879. Prioniodus erraticus, G. J. Hinde, Quart. Jour. Geol. Soc., Vol. XXXV, p. 359, Plate XV, fig. 14.

In such examples as I have procured from the Conodont bed the denticles vary in number, size and spacing, in some specimens being rather widely separated from each other, while in others they are closely crowded together. I figure two specimens which represent the extreme variant from Dr. Hinde's type.

PRIONIODUS ANGULATUS, HINDE

1879. Prioniodus angulatus, G. J. Hinde, Quart. Jour. Geol. Soc., Vol. XXXV, p. 360, Plate XV, fig. 17.

Dr. Hinde says in his description that he collected this species from the Genesee shales in Eighteen Mile Creek at North Evans, New York, and from the Cleveland shales at Bedford, Ohio. Genesee shales do occur at North Evans. They are soft, gray in color and above them lie the black bituminous shales of the Portage group. It was almost certainly from these Portage beds that Dr. Hinde collected his specimens. I have found this species in the Rhinestreet (Portage) shale, near Sturgeon Point, N. Y. It does not seem to occur in the Conodont bed, but certain examples of P. clavatus closely approach it.

PRIONIODUS COLLIGATUS, Spec. Nov.

Plate III, figs. 1, 2 and 4; Plate V, figs. 6 and 10; Plate VI, fig. 8; Plate VII, figs. 2 and 6.

Base long, narrow and more or less arched. Often produced below about the central cavity, from which a groove extends the length of the base. Main cusp short, compressed, and not much larger than the other denticles. These are closely opposed to each other, rather long, flattened and blunt. They are often neatly graduated in height, with hardly any tapering of the individual denticles. They may number as many as eight or ten on either side of the main tooth.

This species is common in the Conodont bed at Eighteen Mile Creek.

PRIONIODUS RETUSUS, Spec. Nov.

Plate IV, figs. 8 and 9; Plate V, figs. 9 and 11; Plate VIII, fig. 3.

A robust species, with short, thick base, arched and produced below the main cusp. This is stout, blunt, circular or ovoid in cross section, as are the robust denticles. There are not more than five or six of these on either side of the main tooth, and they are rather closely arranged and obtusely pointed. This species is not uncommon in the Conodont bed of Eighteen Mile Creek.

PRIONIODUS MURICATUS, Spec. Nov.

Plate V, fig. 7.

Base long and arched, with a pronounced central cavity beneath. From six to nine tenuous pointed denticles are closely arranged on either side of the slender, acute central cusp, which is ovoid in cross section. From the Conodont bed at Eighteen Mile Creek, where perfect specimens are very rare;—the slender and brittle tips of the teeth being nearly always more or less broken. The example figured shows better than any other, the basal cavity beneath the main cusp which is characteristic of all Conodonts. From the Conodont bed of Eighteen Mile Creek.

PRIONIODUS PRAVUS, Spec. Nov.

Plate VIII, fig. 5.

Base long, narrow and strongly arched. Above the arch is a short, compressed, expanded tooth, somewhat bent and very blunt, being wider at the summit than at the base. On one side of this main cusp is a row of thirteen robust denticles, uneven in height, and closely opposed, and on the other side are about eight smaller and likewise uneven denticles. Rare in the Conodont bed of Eighteen Mile Creek.

PRIONIODUS SPATULATUS, Spec. Nov.

Plate VIII, fig. 9.

Base short and arched. Main cusp enormously expanded and compressed, wider about halfway of its height than either above or below, its outer face strengthened by a midrib or keel, and its apex rounded. On either side, a row of three or four stout, sub-cylindrical, blunt denticles. Rare in the Conodont bed of Eighteen Mile Creek.

PRIONIODUS MACRODENTUS, Spec. Nov.

Plate VIII, fig. 10.

Base arched and wide, the margins curled up like the brim of a hat. Near one end a large, robust, spike-shaped fang projects obliquely upward and outward. This main cusp is bordered on one side by a row of about eight large, conical, pointed teeth of varying heights, rather closely arranged, their bases fused together. On the other side there are but one or two smaller denticles. From the Conodont bed of Eighteen Mile Creek.

PRIONIODUS ARMATUS, HINDE

1879. Prioniodus armatus, G. J. Hinde, Quart. Journ. Geol. Soc., Vol. XXXV, p. 360, Plate XV, figs. 20 and 21.

I believe that this species can be found at Eighteen Mile Creek only in rocks of Portage age. It is not uncommon in the Rhinestreet shale, but I have not as yet found it in the Genesee. Its closest ally is P. erraticus.

PRIONIODUS SPICATUS, HINDE

1879. Prioniodus spicatus, G. J. Hinde, Quart. Journ. Geol. Soc., Vol. XXXV, p. 361, Plate XVI, figs. 1, 2, 3.

1886. Prioniodus spicatus, J. M. Clarke, Report of the State Geologist for 1885, Albany, N. Y., Plate A-1, fig. 22.

It is probable that this, like the preceding species, was incorrectly referred by Dr. Hinde to the Genesee. It does not seem to occur in the Conodont bed, but Dr. J. M. Clarke has figured an example from the Portage (Naples beds) in Ontario County, N. Y., and I have collected it from the Rhinestreet shale near Sturgeon Point, N. Y.

PRIONIODUS IMMERSUS, HINDE

Plate VI, fig. 2.

1879. Polygnathus immersus, G. J. Hinde, Quart. Journ. Geol. Soc., Vol. XXXV, p. 364, Plate XVI, fig. 21.

In this species the teeth are set upon a transparent base. The denticles are quite flattened and viewed by transmitted light they appear to be imbedded up to their tips in the base, or to be connected by a thin, transparent web. Part of this appearance is due to the pigmentation of the interior of the denticle, which extends downward into the base. This fusion or union of the denticles by a transparent webbing often occurs in other species of Conodonts. Thus it is found in nearly all of the crest-like teeth terminating the tuberculated plates in the genus Polygnathus. It is also common in specimens of P. radiatus and P. alatus. The photographs taken by reflected light do not show this "immersed" condition very clearly. My specimens which show considerable variation, are all from the Conodont bed; while Dr. Hinde's types were collected from black shales on the Canadian shores of Lakes Erie and Huron.

PRIONIODUS NASUTUS, HINDE.

1879. Polygnathus nasutus, G. J. Hinde, Quart. Journ. Geol. Soc., Vol. XXXV, p. 364, Plate XVI, fig. 22.

This form seems to me to belong in the genus Prioniodus, being allied in the character of the main cusp to P. alatus. Hinde's type came from the shales at Eighteen Mile Creek (Portage?). I have found it or something very like it in the Conodont bed.

PRIONIODUS CRISTATUS, Spec. Nov,

Plate III, fig. 9; Plate VI, fig. 7.

Base more or less sigmoidally arched, narrow and flattened. Viewed from above one end broadly expanded, the other narrow. The expanded end carries a crest-like row of tall, closely crowded and somewhat compressed teeth. These are followed on the narrowed portion of the base by a row of very short blunted denticles. On the underside of the base, beneath the largest of the crested teeth is a lozenge-shaped cavity, from which a groove runs to either end.

As in all of the species of the genus the number of the denticles is variable, and in some specimens the expanded end is abruptly depressed.

From the Conodont bed at Eighteen Mile Creek, Erie County, N. Y.

PRIONIODUS OBTUSUS, Spec. Nov.

Plate III, fig 6; Plate VI, fig. 1.

Base narrow, straight for the greater part of its length, with one end deflected downward. Main tooth very broad, compressed, blunted, wider above than below, and produced into a spur beneath the base. On one side of this main cusp are arranged a number of tall slender denticles; on the other side, the denticles are short, crowded, robust and obtuse.

I collected this form from the Conodont bed, where it is rather uncommon.

PRIONIODUS DILATUS, Spec. Nov.

Plate VII, figs. 3, 4 and 11.

Base as seen from the side with a somewhat sigmoidal curvature. As seen from above one end is narrow, the other very broad and expanded; the widest portion of the plate being not far from the extremity. This base supports a single row of stout, well-spaced, conical teeth. The underside is very deeply and widely excavated, the cavity being larger and deeper than in any other Conodont known to me.

In the examples here figured the teeth are mostly broken but the basal cavity is directly beneath the largest tooth of the series on the widest portion of the plate and probably extends a short distance into it. I have collected several specimens of this rare species from the Conodont bed at Eighteen Mile Creek, Erie County, N. Y.

PRIONIODUS PARVULUS, Spec. Nov.

Plate IX.

In the upper layers of the Genundewah limestone, Conodonts are rare. The specimens illustrated on Plate IX seem to represent a single new and distinct species and may very well have belonged to one individual as they were found associated together on a slab less than three inches square, which I collected from the upper surface of this limestone.

The base in this species is short, slightly arched, and somewhat convex. It supports at one end a short wide and robust tooth, following which is a series of stout and obtuse denticles sometimes but little inferior in size to the main cusp. A single denticle is usually attached to the outer side of the principal tooth.

This is one of the smallest species of the genus. My figures show the variations which may, perhaps, occur in the teeth of one individual. In some specimens the main cusp is hardly to be distinguished from the following denticles, while in other examples it is quite pronounced.

CENTRODUS CORONATUS, HINDE

1879. Polygnathus coronatus, G. J. Hinde, Quart. Journ. Geol. Soc., Vol. XXXV, p. 365, Plate XVII, fig. 1.

I see no reason for placing this form with Polygnathus. It possesses all the characters of Pander's genus Centrodus and, as Hinde himself remarks, is very close to Centrodus convexus. In fact, Pander included within the same species much more variable forms than these two. Hinde refers this species to the Genesee shales, but it probably came from the Portage. I have specimens of it from the Rhinestreet shales at Sturgeon Point, N. Y.

CENTRODUS INVALIDUS, Spec. Nov.

Plate III, figs. 3 and 5.

This form very closely resembles Pander's Centrodus simplex, and certain of the pectinate teeth included in the group which Hinde named Polygnathus dubius. It is quite possible that all of these teeth may have belonged to one individual, but equally possible that their association together may have been the result of their original owners, perhaps of several genera, having become the food of contemporaneous, larger fishes. I once collected a slab of Rhinestreet shale, which within the space of four square inches contained a great many Conodonts, together with crushed and broken integumentary plates and a few Lingula valves. The specimen contained many, but by no means all of the forms figured by Hinde and Clark, as Polygnathus dubius, together with teeth which have been described under different genera and species.

If these Conodonts all belonged to one individual, the animal must have been so large that it is astonishing that no other traces of it have been found in these shales which preserve so beautifully the delicate tissues of plants and other fragile objects.

In the present uncertainty, even as to the class of animals which bore these teeth, it seems to me advisable to retain Pander's generic names for forms described by him, and to restrict Hinde's genus Polygnathus to those crested crushing or tritoral plates so characteristic of his type specimen.

The species figured herein on Plate III, figs. 3 and 5, differ from Centrodus simplex and from the forms illustrated by Hinde, in that the base is more arched and rounded, and the teeth are shorter and more variable in size.

From the Conodont bed in Eighteen Mile Creek.

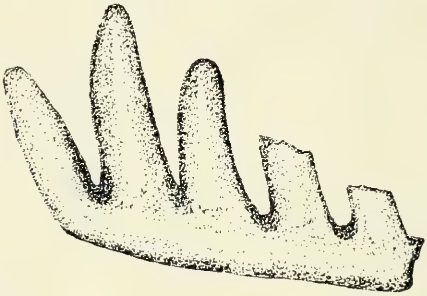


Fig. 6. Centrodus princeps, Hinde. × 30.

CENTRODUS PRINCEPS, HINDE

Text Fig. 6.

1879. Polygnathus princeps. G. J. Hinde, Quart. Journ. Geol. Soc., Vol. XXXV, p 365, Plate XVI, fig. 23.

For the reasons given above, I refer this species to Pander's genus Centrodus. It may even be a variety of his C. simplex, differing merely in the more robust and blunted denticles. Fig. 6 shows one end of a broken specimen; Hinde's type lacks both ends.

GNATHODUS AMERICANUS, Spec. Nov.

Plate VII, fig. 5.

This genus, transitional between the narrow-based pectinate forms like Prioniodus and the broad-based tuberculated tritoral plates of Polygnathus, has hitherto been known by a solitary species described by Pander from the marl in the vicinity of Moscow. It illustrates the progressive adaptation of the basal portion of the plate into a grinding tritor. In Polygnathus this transformation is complete, the pectinate ridge either disappearing or being confined to a crest projecting beyond the tritor.

A form very close to Gnathodus mosquensis occurs in the Conodont bed and I propose to name this species, the first to be discovered in this country, Gnathodus americanus.

For about one-half of its length the base expands and curls upward like a withered leaf. Its upper surface bears a number of prominent tubercules. Surmounting the base is a long, thin ridge of flat coalesced teeth unequal in heighth. The cavity beneath the base is centrally located, of the usual lozenge shape and much smaller than that in Gnathodus mosquensis.

POLYGNATHUS PENNATUS, HINDE

Plate X, figs. 1 to 9.

1879. Polygnathus pennatus, G. J. Hinde, Quart. Journ. Geol. Soc., Vol. XXXV, p. 366, Plate XVII, fig. 8.

1879. Polygnathus dubius, G. J. Hinde (in part), Quart. Journ. Geol. Soc., Vol. XXXV, p. 363, Plate XVI, fig. 17.

1886. Polygnathus dubius, J. M. Clarke, 6th Annual Report, N. Y. State Geologist, Plate A-1, figs. 2, 3, 13.

1886. Polygnathus pennatus, J. M. Clarke, 6th Annual Report, N. Y. State Geologist, Plate A-1, fig. 9.

The genus Polygnathus was established by Dr. Hinde to receive Conodonts of various forms associated together on a single slab of shale probably of Portage age, and considered by him to have belonged to the same animal. I have given in another place my reasons for doubting the propriety of including in one genus all of these forms, some of which had already been described under various genera. If, for no other reason than convenience in classification, in the present state of our knowledge, I believe the genus Polygnathus should be restricted, so as to include only those tuberculated and rugose tritoral plates discovered for the first time with the type specimen and characteristic of it. These consist of leaf-shaped plates with a central rib or ridge which is produced beyond the tritoral margin into a stem-like flattened crest of pectinate teeth. P. pennatus is the smallest and one of the commonest of these forms. It ranges in geologic time from the base of the Genesee to the Rhinestreet shale in the Portage group. Specimens are abundant in the Conodont bed, but many of the other forms described together with it as Polygnathus dubius are absent.

Dr. Hinde figured a side view of a specimen of this species to accompany his description of P. dubius and in the same article figured as P. pennatus an upper view of the same species. Both of these specimens, although referred to the Genesee were probably collected from the Portage shales. Owing to their peculiar shape these fossils have a deceptive appearance when variously oriented in the matrix and it is not surprising that Dr. Hinde and later, Dr. Clarke, failed to recognize them in their different aspects when imbedded in the shales. I have figured on Plate X, figs. 1-9, examples of this species in various aspects. Figs. 6 and 8 are views of the underside, showing the diamond-shaped cavity common to all Conodonts from this region. It will be noted that rights and lefts can easily be distinguished.

POLYGNATHUS CRISTATUS, HINDE

1879. Polygnathus cristatus, G. J. Hinde, Quart. Jour. Geol. Soc., Vol. XXXV, p. 366, Plate XVII, fig. 11.

1879. Polygnathus dubius, G. J. Hinde, Quart. Journ. Geol. Soc., p. 363 (crested teeth), Plate XVI, figs. 16, 18.

1886. Polygnathus cristatus, J. M. Clarke, Report of the State Geologist of New York, Plate A-1, fig. 20.

1886. Polygnathus dubius, J. M. Clarke, Report of the State Geologist of New York, Plate A-1, fig. 1.

This, like the preceding species, was described under two names by Dr. Hinde, but there can be no question that his drawings as well as those of Dr. Clarke are of different aspects of the same form. Both Hinde and Clarke have figured upper and profile views. The upper surface of the plate is ornamented on each side of the central ridge with a double row of tubercules which have a tendency to a linear arrangement. The species occurs in the Portage group, and Hinde described it from the Conodont bed, but if it actually came from there, it must be so rare that it has not appeared in later collections. I suspect that it came from a Portage shale locality.

POLYGNATHUS ORDINATUS, Spec. Nov.

Plate X, figs. 10, 11.

Plate lanceolate in outline, the upper surface convex in its longest axis, and deeply grooved longitudinally. A crenulated central crest arises from this groove, and is produced beyond one end of the plate. The main plate is ornamented with tubercules, often grouped in one or two longitudinal rows on either side of the crest.

Conodont bed of Eighteen Mile Creek.

POLYGNATHUS FOLIATUS, Spec. Nov.

Plate X, figs. 13-16.

Dental plate narrowly lanceolate, its margins curled upward like a slightly withered leaf. In profile the plate is sigmoidal in outline, while viewed from above there is a longitudinal medial furrow, from which arises a slender, crenulated keel. This keel extends beyond the main plate as an expanded process, armed above with a few serrations. The upper surface of the main plate is covered with minute tubercules.

Conodont bed of Eighteen Mile Creek.

POLYGNATHUS PERACUTUS, Spec. Nov.

Plate X, fig. 12.

Plate triangular in outline, convex in its longest axis and relatively flat or slightly arched transversely. No longitudinal central furrow, and the usual central crest indicated only by a median row of elongated tubercules. An expanded appendage with prominent crenulations or teeth projects beyond the main plate. Upper surface of main plate covered with closely arranged tubercules.

Conodont bed of Eighteen Mile Creek.

POLYGNATHUS PUNCTATUS, HINDE

1879. Polygnathus punctatus, G. J. Hinde, Quar. Jour. Geol. Soc., Vol. XXXV, p. 367, Plate XVII, fig. 14.

This species was described by Hinde as occurring in the Genesee shale of Eighteen Mile Creek. I have never found it in the Conodont bed, and I believe it must be a Portage species or even younger, as Dr. Ulrich has informed me that he has found it, or a closely related form, in the Chattanoogan shales.

POLYGNATHUS LINGUIFORMIS, HINDE

Plate XI, figs. 1-9; Plate XIV, fig. 2.

1879. Polygnathus linguiformis, G. J. Hinde, Quart. Journ. Geol. Soc., Vol. XXXV, p. 367, Plate XVII, fig. 15.
1879. Polygnathus simplex, G. J. Hinde, Quart. Journ. Geol. Soc., Vol. XXXV, p. 367, Plate XVII, fig. 18.

I illustrate on Plate XI upper views of a number of paired plates, the rights and lefts being easily distinguished; and in fig. 9 a profile view of the same species. It is hardly to be wondered that Dr. Hinde with only specimens in the matrix at his command, should have referred differently oriented examples to distinct species. The tongue-like process is ornamented on its upper surface with parallel raised lines which sometimes break up into tubercules on the elevated portion of the plate. Specimens of this species on account of their twisted shapes are difficult to photograph. All my specimens are from the Conodont bed. Dr. Hinde also reports it from the Genesee (?) shale on the north shore of Lake Erie, Ontario.

POLYGNATHUS TUBERCULATUS, HINDE

Plate XII, figs. 7-9.

1879. Polygnathus tuberculatus, G. J. Hinde, Quar. Jour. Geol. Soc., Vol. XXXV, p. 336, Plate XVII, fig. 9.

Hinde figured two specimens under this name. Of these, the original of his figure 9, according to his description, is clearly to be accepted as the type. His figure 10 represents the reverse side of a form which is described in this paper under the name of Polygnathus rotundilobus.

The upper surface of Polygnathus tuberculatus is convex and sculptured with tubercules and rugosities which have a tendency to radiate from the center of the plate. In my specimens there is hardly ever a prolonged central keel. More often it occurs only at one end of the plate, beyond which it projects from a deep notch, as a stout process, armed with sharp teeth. On either side of this notch is a narrow basal lobe, each with an oblique nodose ridge.

Conodont bed, Eighteen Mile Creek.

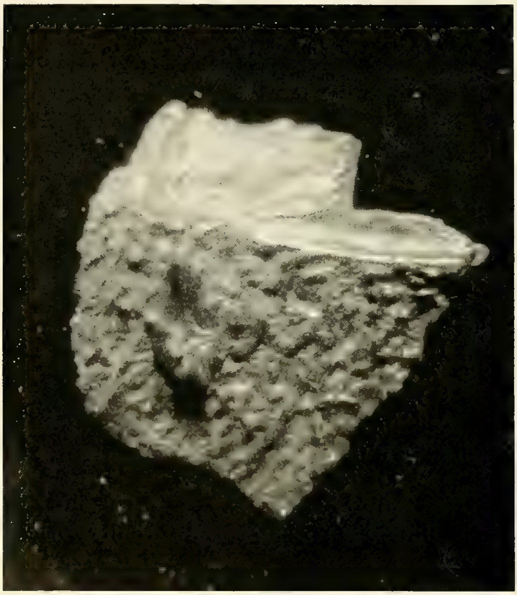


Fig. 7. Polygnathus rotundilobus, Bryant. Associated with fish plate × 14.

POLYGNATHUS ROTUNDILOBUS, Spec. Nov.

Plate XII, figs. 1-6; Text fig. 7.

1879. Polygnathus tuberculatus, G. J. Hinde (in part), Quar. Jour. Geol. Soc., Vol. XXXV, p. 366, Plate XVII, fig. 10.

This is a robust but graceful form. The main plate is roughly triangular with rounded lateral lobes. The tritoral surface is convex and is armed with clusters of tall, conical tubercules, while the underside is smooth and polished, with the usual central diamond-shaped pit, from which a furrow extends beneath the produced keel. This keel bears upon its summit a few very stout, compressed teeth. I have figured various aspects of these plates which are all from the Conodont bed. Text figure 7 shows a specimen cemented by its upper surface to a fragmentary plate of an undescribed fish, perhaps an Arthrodire.

The nearest related form to this species is Polygnathus crassus, Hinde, described from a plate seen in profile. It is even possible that the species are identical.

The specimen figured by Hinde on his Plate XVII, fig. 10, as probably belonging to Polygnathus tuberculatus is no doubt the reverse side of this species.

POLYGNATHUS CÆLATUS, SPEC. NOV.

Plate XIII, figs. 1-13.

Plates large and massive attaining a length of three millimeters. Irregular in outline, sometimes diamond-shaped, sometimes sigmoidal, with a prominent medium keel of robust teeth or tubercules. Superficial ornament consisting of prominent elongated nodes or tubercules and ridges usually disposed at right angles to the central keel and extending to the margin.

While there is considerable variation among these plates, their robust proportions and general aspect lead me to believe that they may all be referred to the same species. This is the largest form on record. My examples all came from the Conodont bed at Eighteen Mile Creek, Erie County, N. Y.

POLYGNATHUS SOLIDUS, HINDE

Plate VII, figs. 7-10, 12.

1879. Polygnathus solidus, G. J. Hinde, Quart. Journ. Geol. Soc. Vol. XXXV, p. 365, Plate XVII, fig. 2.

Although this form differs from the typical Polygnathus in the absence of a tritor, yet because of its resemblance to the terminal crests of most species of this genus, I believe Dr. Hinde was correct in placing it therein. Some specimens may, indeed, be such detached crests but certain of them have a basal pit centrally located, indicating that the plates are entire. The form is typical of the Conodont bed.

The following forms described by Dr. Hinde as from the Genesee shales probably occur only in the Portage. At least a careful search extending over several years has failed to locate them in the rocks of Genesee age.

Polygnathus ? duplicatus.
Polygnathus ? serratus.
Polygnathus ? criensis.
Polygnathus curvatus.
Polygnathus palmatus.

PLATE I

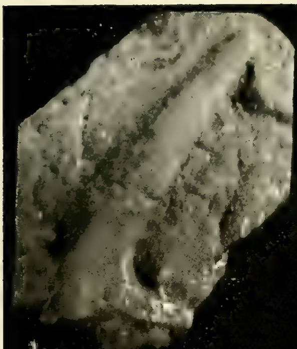
Fig. 1. Prioniodus recedens, Bryant. Tooth in matrix. × 20.

Fig. 2, 6-14. Prioniodus recedens, Bryant. × 25.

Figs. 3-5. Prioniodus abbreviatus, Hinde. × 25.

All of the originals figured on this plate are from the Conodont bed (basal Genesee), in Eighteen Mile Creek, Erie County, N. Y.

PLATE I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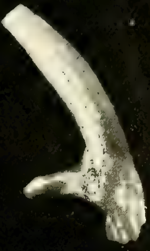
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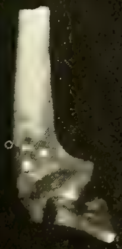
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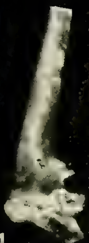
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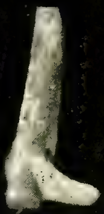
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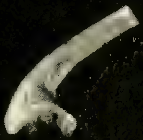
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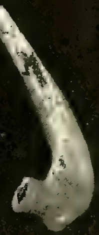
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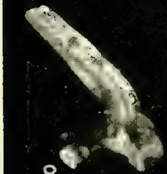
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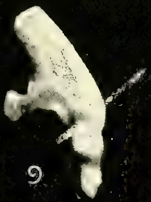
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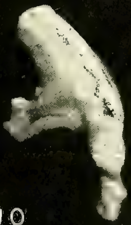
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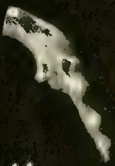
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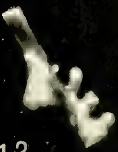
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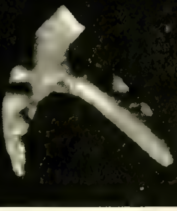
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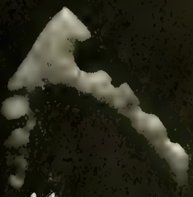
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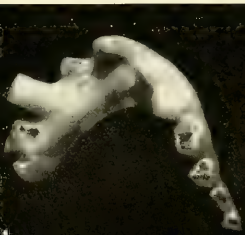
PLATE II

Figs. 1-4, 7, 9. Prioniodus recedens, Bryant. × 25.

Figs. 5, 6, 8, 11. Prioniodus hamatus, Bryant. × 25.

Fig. 10. Prioniodus erraticus, Hinde. × 25.

All of the originals figured on this plate are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.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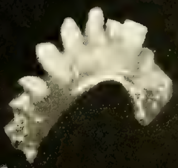
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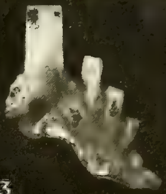
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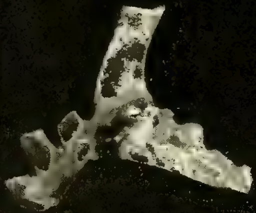
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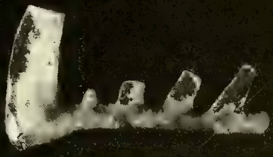
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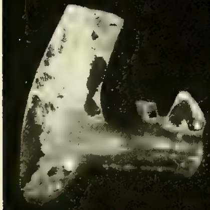
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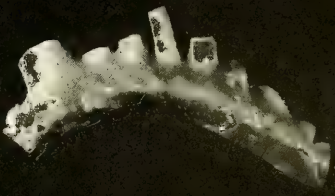
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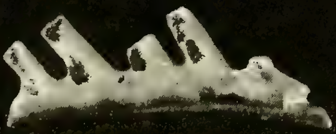
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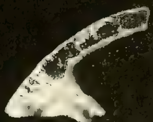
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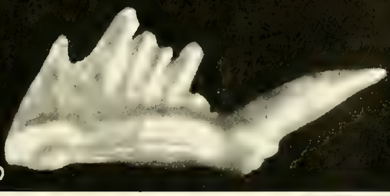
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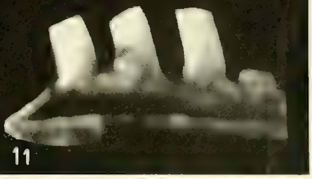
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PLATE III

Figs. 1, 2, 4. Prioniodus colligatus, Bryant.

Figs. 3, 5. Centrodus invalidus, Bryant.

Fig. 6. Prioniodus obtusus, Bryant.

Fig. 7. Prioniodus abbreviatus, Hinde. Thin section showing dimensions of basal cavity.

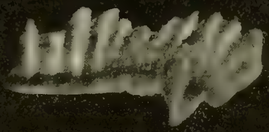
Fig. 8. Conodont fractured so as to exhibit internal pigmentation of denticles.

Fig. 9. Prioniodus cristatus, Bryant.

Fig. 10. Prioniodus alatus, Hinde.

Originals from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y. Figs. 2, 3, 5, 6, 7, × 30. All others × 25.

PLATE III



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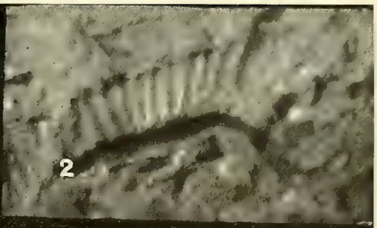

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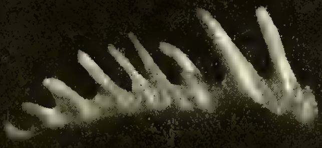

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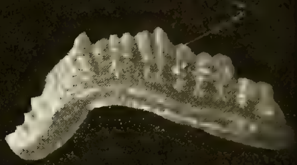

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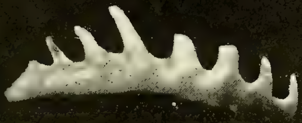

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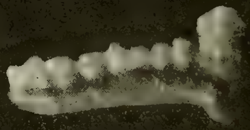

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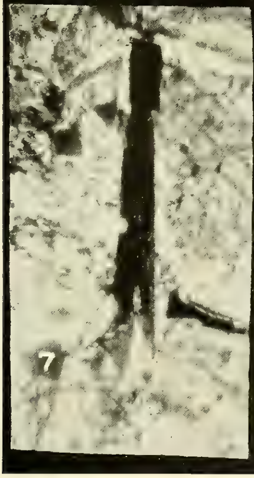

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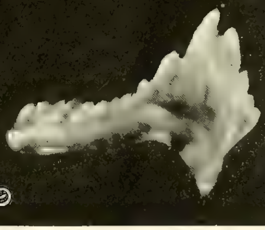

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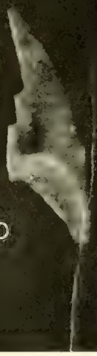

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PLATE IV

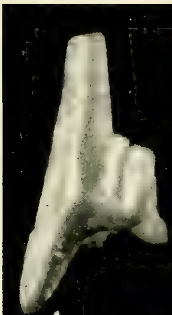
Figs. 1-7. Prioniodus alatus, Hinde. × 25.

Figs. 8-9. Prioniodus retusus, Bryant. × 25.

Figs. 10-12. Prioniodus radiatus, Hinde. × 25.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.

PLATE IV



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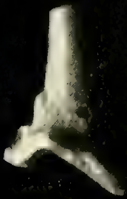

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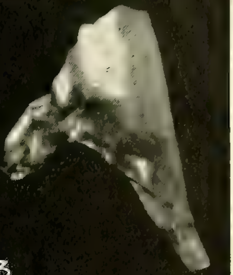

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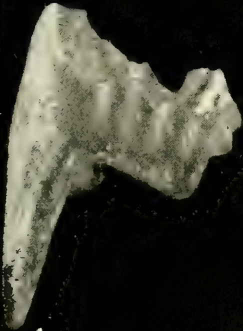

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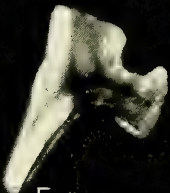

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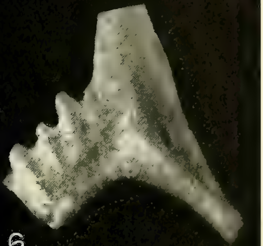

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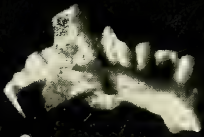

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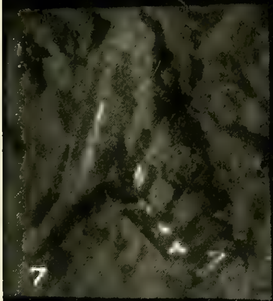

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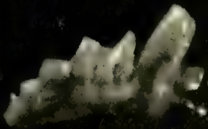

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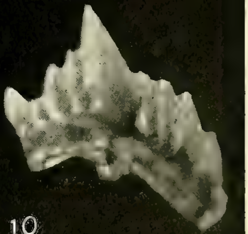

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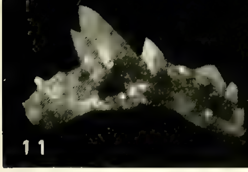

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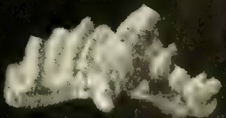

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PLATE V

Figs. 1-5, 8. Prioniodus radiatus, Hinde. × 25.

Fig. 6. Prioniodus colligatus, Bryant. × 30.

Fig. 7. Prioniodus muricatus, Bryant. × 25.

Fig. 10. Prioniodus colligatus, Bryant. ×25.

Figs. 9, 11 Prioniodus retusus, Bryant. × 30.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.

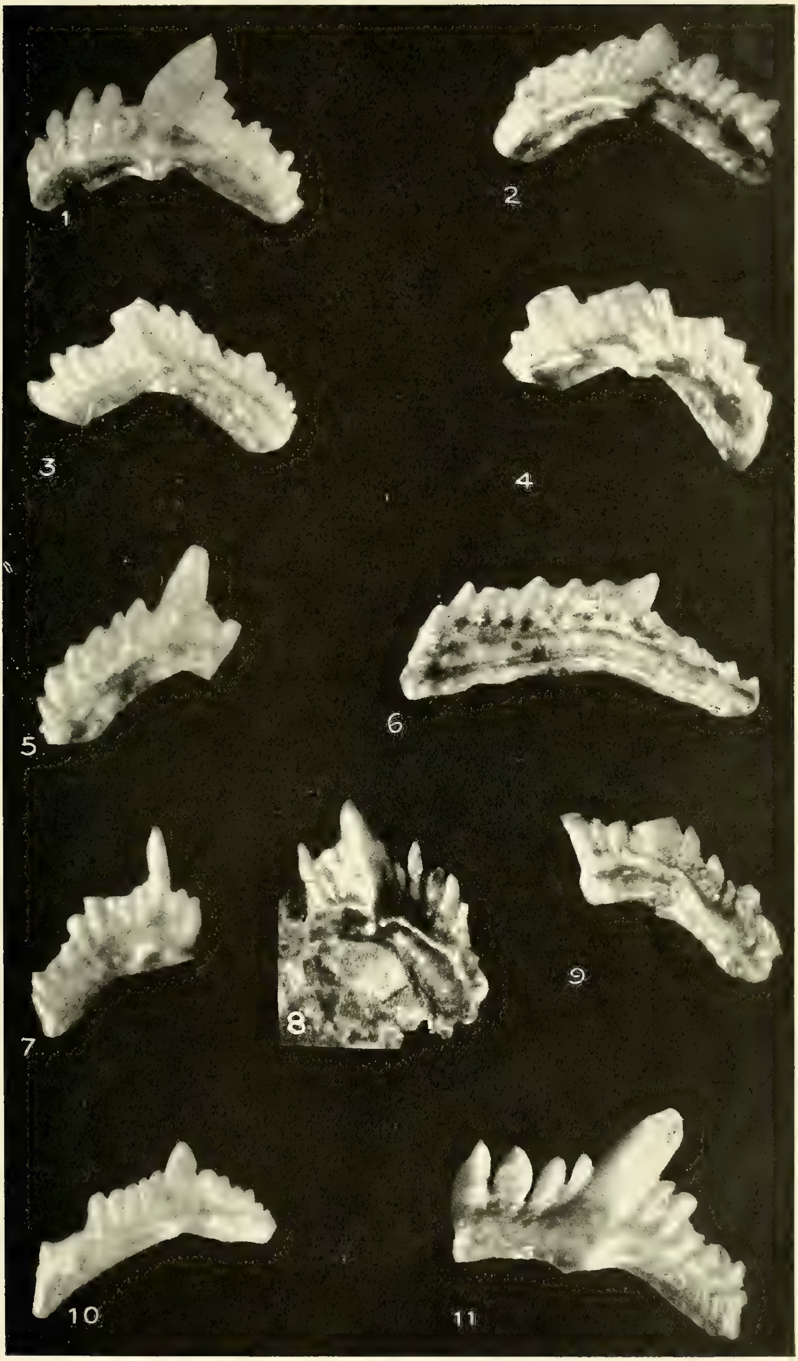
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PLATE VI

Fig. 1. Prioniodus obtusus, Bryant. × 30.

Fig. 2. Prioniodus immersus, Hinde. × 25.

Fig. 3. Prioniodus clavatus, Hinde. × 30.

Fig. 4. Prioniodus spicatus, Hinde. × 30.

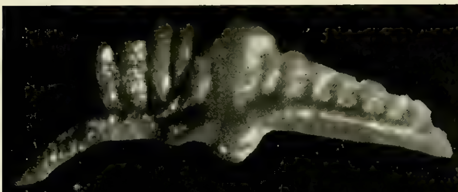
Fig. 5. Prioniodus radiatus, Hinde. × 30.

Fig. 6. Prioniodus clavatus, Hinde. × 25.

Fig. 7. Prioniodus cristatus, Bryant. × 40.

Fig. 8. Prioniodus colligatus, Bryant. × 30.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.



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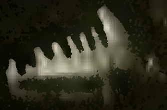

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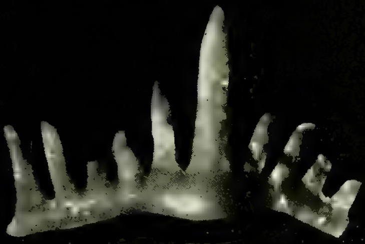

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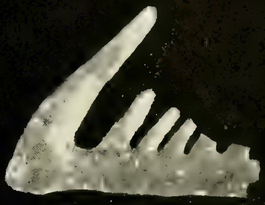

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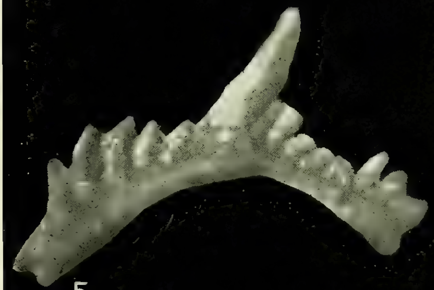

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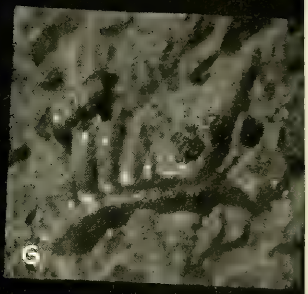

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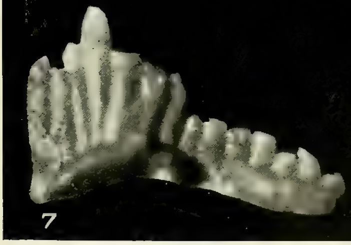

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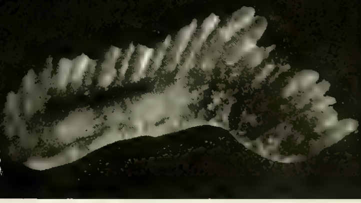

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PLATE VII

Fig. 1. Prioniodus erraticus, Hinde. × 20.

Figs. 2, 6. Prioniodus colligatus, Bryant. × 20.

Figs. 3, 11. Prioniodus dilatus, Bryant. × 25.

Fig. 4. Prioniodus dilatus, Bryant, showing excavation of the underside. × 20.

Fig. 5. Gnathodus americanus, Bryant. × 20.

Figs. 7-10, 12. Polygnathus solidus, Hinde. × 20.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.

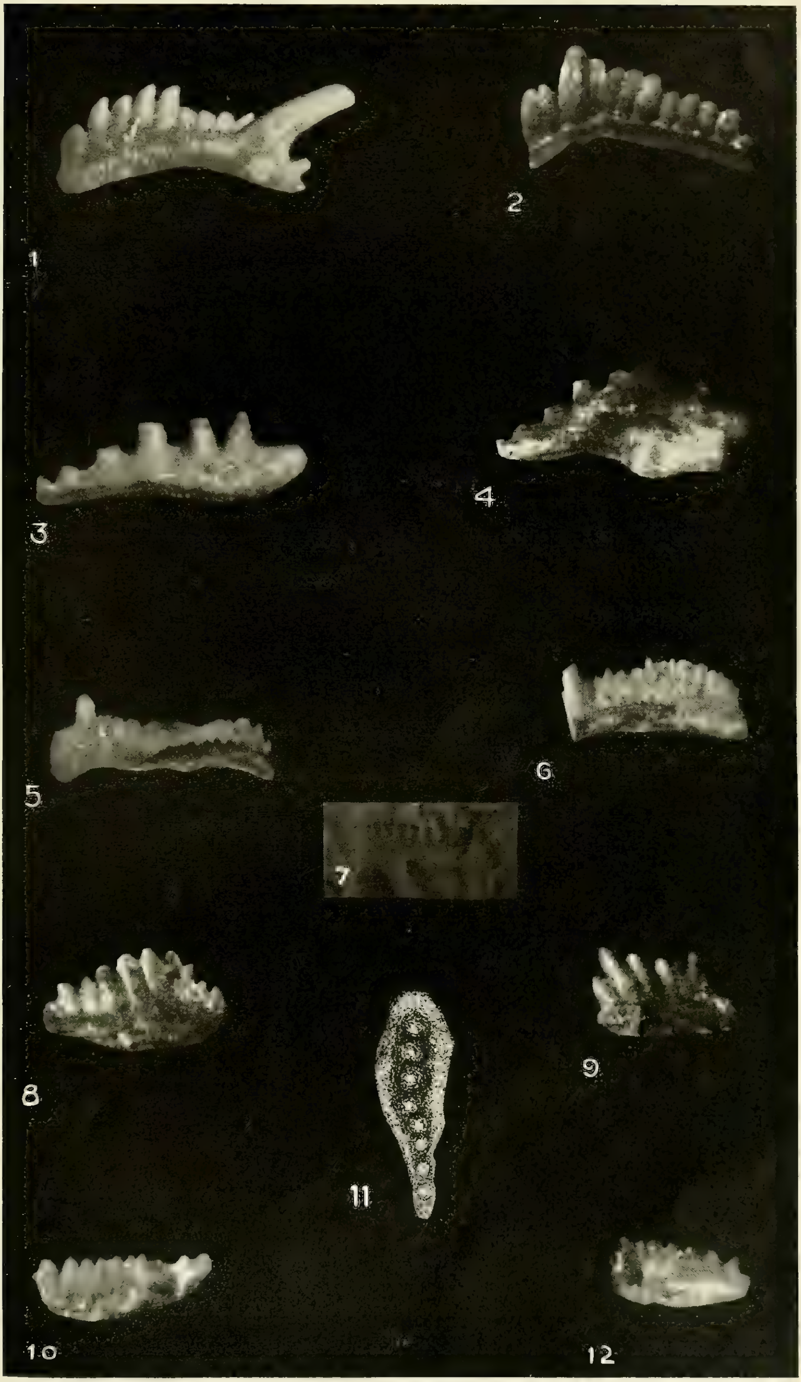
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PLATE VIII

Fig. 1, 2, 4, 6-8. Prioniodus radiatus, Hinde. × 25.

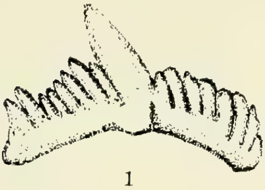
Fig. 3. Prioniodus retusus, Bryant. × 25.

Fig. 5. Prioniodus pravus, Bryant. × 25.

Fig. 9. Prioniodus spatulatus, Bryant. × 25.

Fig. 10. Prioniodus macrodentus, Bryant. × 25.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.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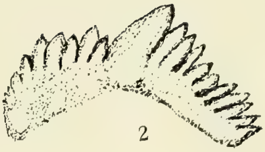
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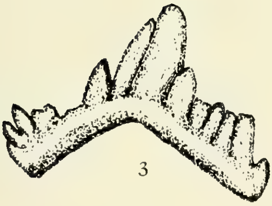
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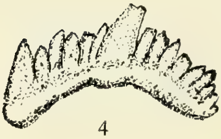
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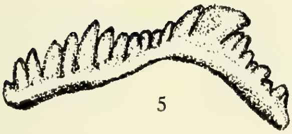
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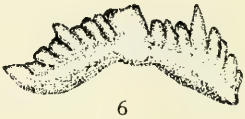
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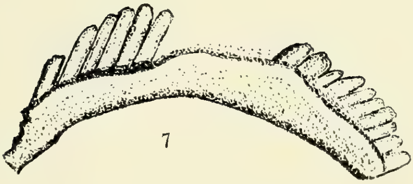
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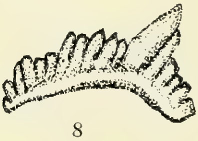
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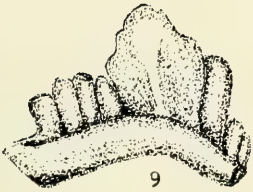
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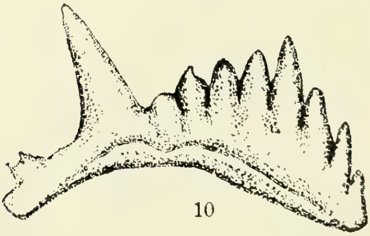
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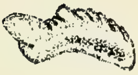
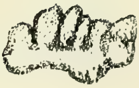
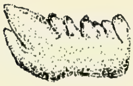
PLATE IX

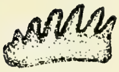
Prioniodus parvulus, Bryant. × 20.

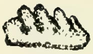
Originals are from the Genundewah limestone (Genesee) in Eighteen Mile Creek, Erie County, N. Y.

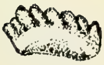


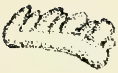












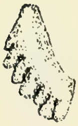


PLATE X

Figs. 1-9. Polygnathus pennatus, Hinde. × 20.

Figs. 10-11. Polygnathus ordinatus, Bryant. × 20.

Fig. 12. Polygnathus peracutus, Bryant. × 18.

Figs. 13-16. Polygnathus foliatus, Bryant. × 20.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.

PLATE X

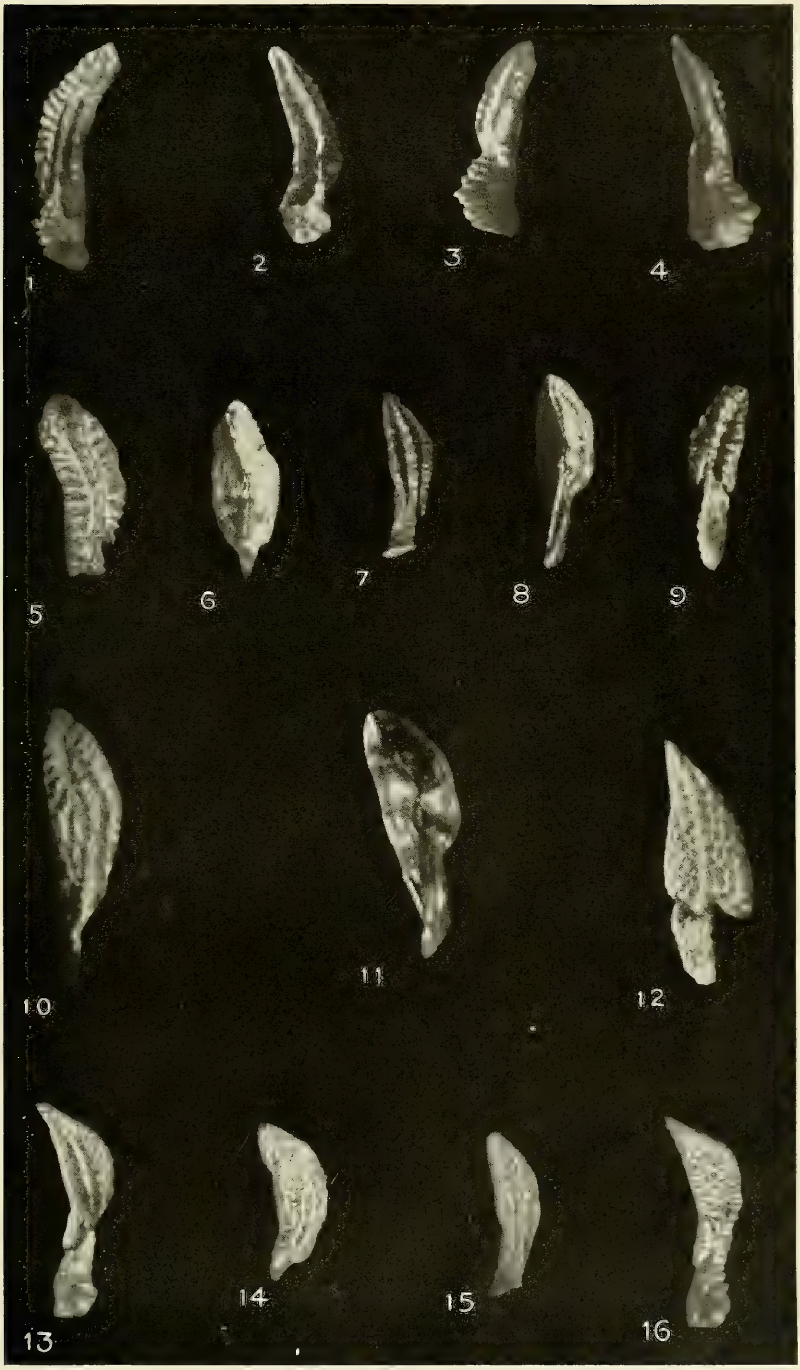
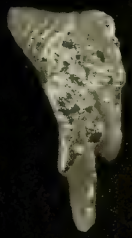


PLATE XI

Figs. 1-9. Polygnathus linguiformis, Hinde. × 20.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.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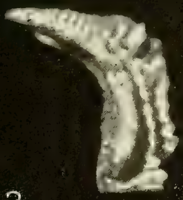
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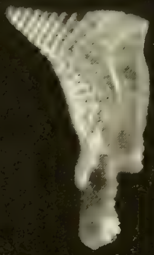
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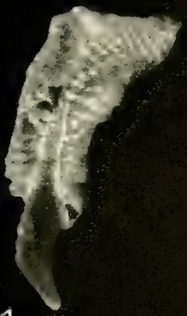
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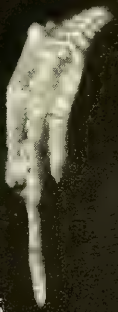
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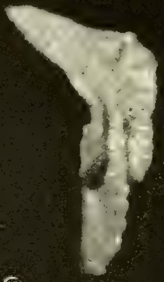
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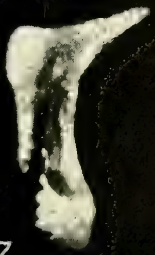
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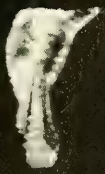
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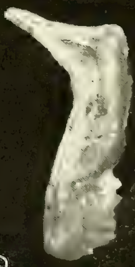
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PLATE XII

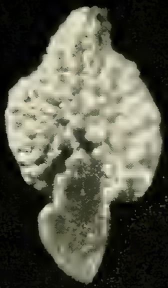
Figs. 1-5. Polygnathus rotundilobus, Bryant. × 18.

Fig. 6. Polygnathus rotundilobus, Bryant. × 20.

Figs. 7-9. Polygnathus tuberculatus, Hinde. × 20.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.

PLATE XII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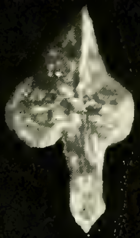
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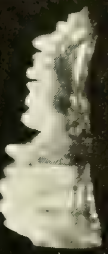
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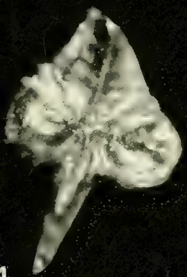
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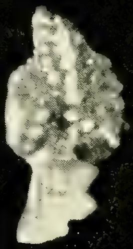
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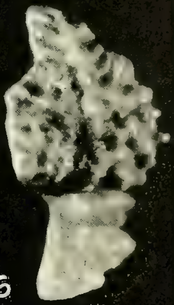
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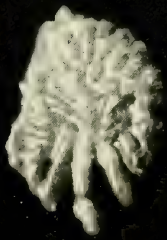
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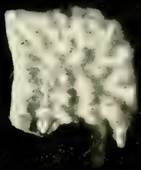
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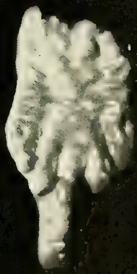
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PLATE XIII

Figs 1, 4, 5, 7, 9, 11-13. Polygnathus cælatus, Bryant. × 18.

Figs. 2, 5, 6. Polygnathus cælatus, Bryant. × 12.

Figs. 3, 10. Polygnathus cælatus, Bryant. × 15.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.

PLATE XIII

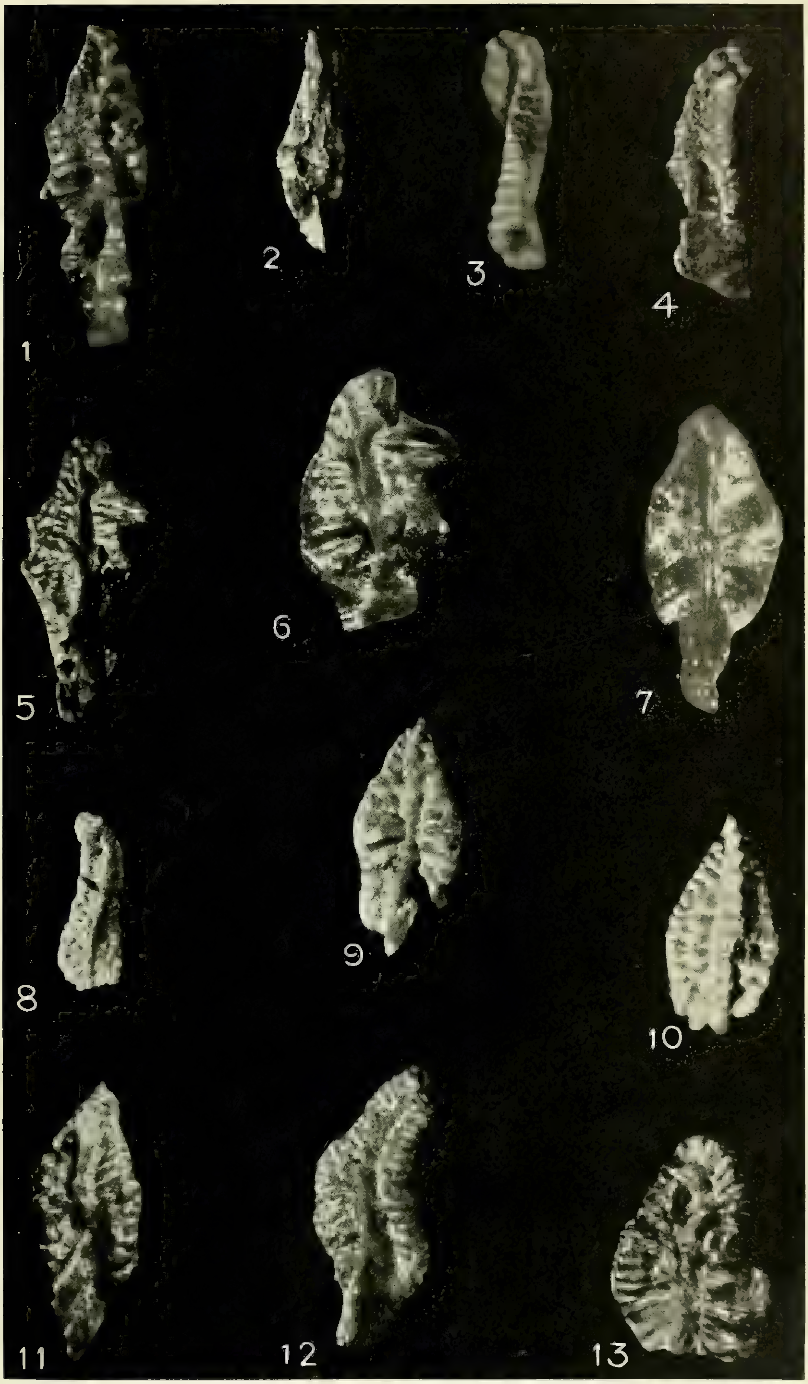


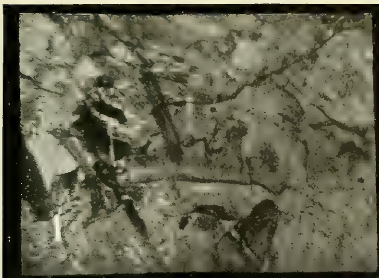
PLATE XIV

Fig. 1. Prioniodus radiatus, Hinde. Thin section. × 20.

Fig. 2. Polygnathus linguiformis, Hinde. Thin section. × 20.

Figs. 3-7. Sculptured dermal plates found in association with Conodonts. × 25.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.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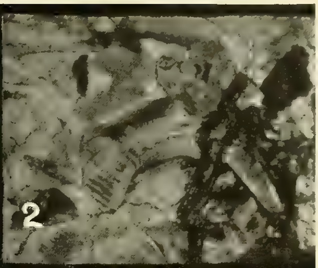
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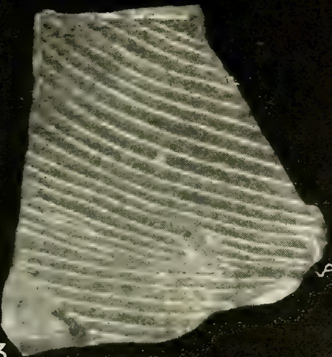
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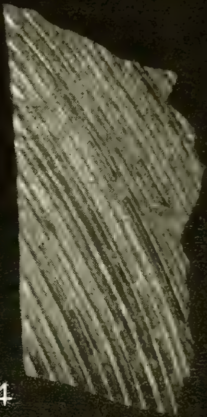
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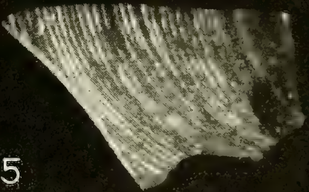
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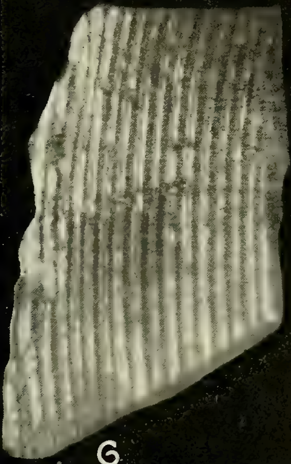
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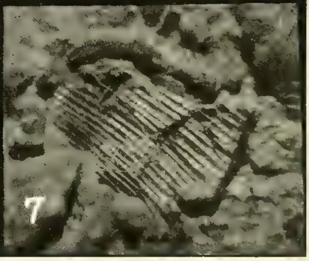
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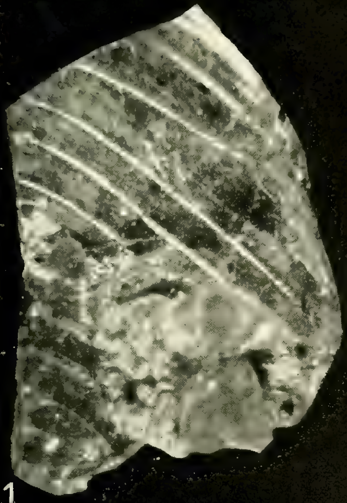
PLATE XV

Fragmentary dermal (?) plates found in association with Conodonts. × 25.

Fig. 3. Shows the under surface of one of these plates.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.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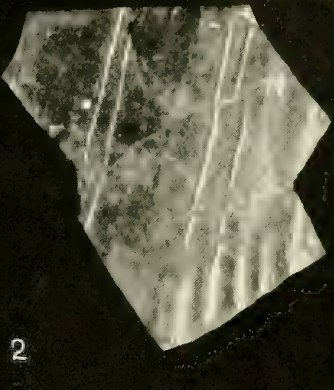
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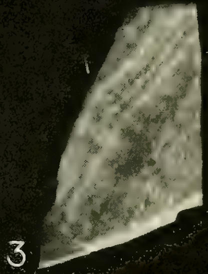
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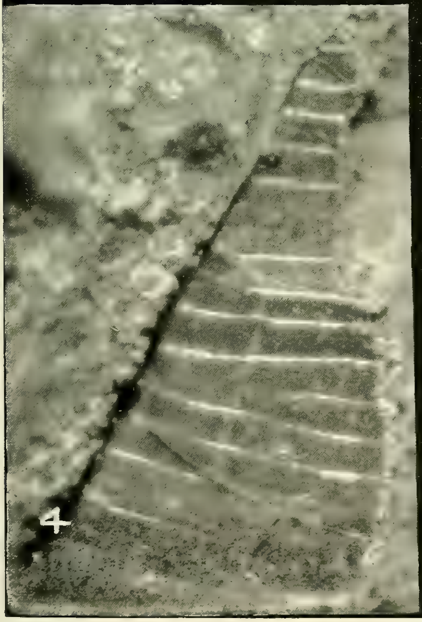
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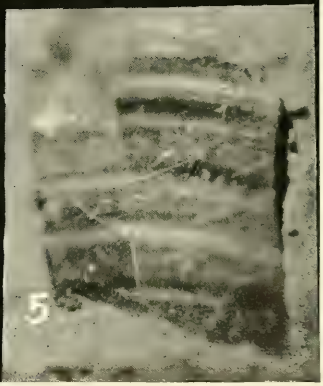
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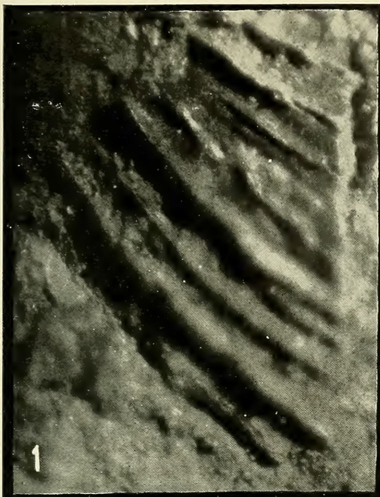
PLATE XVI

Figs. 1-6. Sculptured dermal (?) plates found in association with Conodonts. × 25.

Originals are from the Conodont bed (Genesee) in Eighteen Mile Creek, Erie County, N. Y.

PLATE XVI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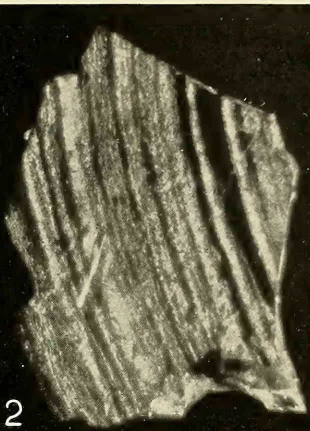
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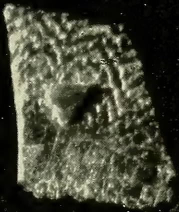
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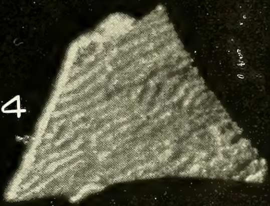
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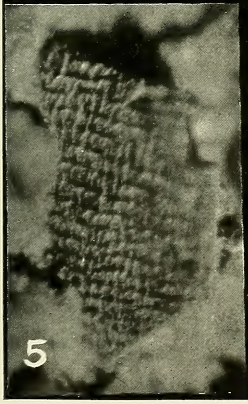
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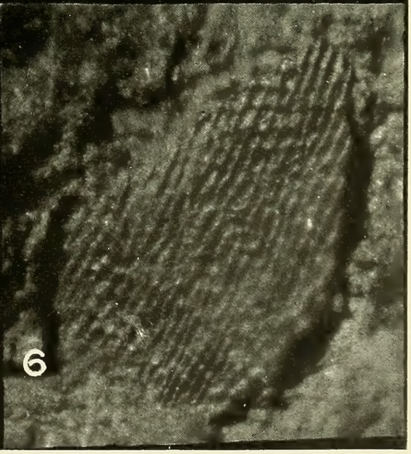
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